EFFECTS OF SLOPE ON THE DYNAMICS OF A TROPICAL MONTANE OAK-BAMBOO FOREST IN COSTA RICA

By

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To my father.

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EFFECTS OF SLOPE ON THE DYNAMICS OF A TROPICAL MONTANE OAK-BAMBOO FOREST IN COSTA RICA

By

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Research was conducted in the upper Rio Macho watershed, near Villa Mills (2850 m), Cordillera de Talamanca, Costa Rica, in a relatively homogeneous old-growth oak-bamboo forest on stable slopes not affected by large-scale disturbances, such as landslides. Physiognomically, the evergreen forest is tall, densely stocked, and composed of approximately 40 woody tree species. It is dominated by _Quercus copeyensis_ Corn. Mueller and _Quercus costaricensis_ Liebmann, with a dense _Chusquea_ spp. bamboo understory.

I hypothesized that different slope gradients induce differential local forest dynamics. This overall hypothesis was broken down into a series of testable hypotheses grouped into three thematic sets: effect of slope on tree geometry (tree leaning and crown eccentricity), tree population dynamics (growth, recruitment, and mortality), and gap-phase processes (gap frequency). The study required large-scale monitoring of the forest, achieved by means of 21 permanent 1-ha plots randomly distributed among three slope classes over an area of 20 km^2.

Down-slope tree leaning was correlated with slope angle but was independent of aspect. This pattern was demonstrated by trees of all sizes, including seedlings. As both wind and soil creep failed to explain the observed pattern, the underlying process is hypothesized to be a geoplagiotropic growth response to the asymmetric light environment on slopes. Moreover, mature trees displayed down-slope eccentricity of crowns, hypothesized to result from plagiotropic crown development away from overtopping neighbors.

Relative growth rates of trees were positively correlated with slope and were roughly double those on flat ground. The number of trees growing into the 10 cm diameter class was positively correlated with slope inclination, strongly suggesting that stand turnover is higher on slopes. Nevertheless, mortality rates did not differ among slope inclinations. This was attributed to the small sample size coupled with a high variance of mortality encountered over the rather short monitoring time.

Preliminary results from a gap frequency study currently in progress showed that forests on steep slopes also had higher percentage of their area in gap-phase than forests on flat ground. This further supports the findings that the oak-bamboo forest is more dynamic on slopes than on flats.

CHAPTER 1
INTRODUCTION

Background

The largest tracts of primary forests remaining in Costa Rica are inaccessible high-elevation forests in the Cordillera de Talamanca (Hartshorn et al. 1982, Sader and Joyce 1988). These forest communities are predominantly composed of montane oak-bamboo forests (Holdridge et al. 1971), confined to elevations ranging from approximately 2000 to 3400 m (Blaser 1987, Orozco 1991). Several plant associations have been identified among these oak-bamboo forests (Kappelle et al. 1989), and Kappelle et al. (1991) recorded 483 native woody species in the high areas of the Cordillera de Talamanca (2000 to 3819 m).

Once disturbed, these high-elevation forests recover slowly; they represent some of the tropics' most fragile ecosystems (Ewel 1980). Because of this fragility and their crucial hydrological functions (i.e., provision of drinking water, hydroelectric power, and irrigation water), it has been proposed that high-elevation Costa Rican forests, especially in critical catchments, should receive absolute protection as "Hydrological Reserves" (Hartshorn et al. 1982). As elsewhere in the tropics, however (Myers 1984), degradation of these forests by human impact is rampant and large-scale clearing, chiefly along roads, is substantial despite protective legislation. Deterioration of these forests constitutes a national ecological threat (Hartshorn et al. 1982) with ultimately detrimental economic consequences.

In light of current economic pressures, and despite their protection values, the preservation of such large montane forest tracts in Costa Rica and elsewhere is not feasible without taking into account the potential production functions of these resources (Putz 1988, Wyatt-Smith 1987). Forest conservation strategies that encompass both protection and production are needed (Leibundgut 1982, Pedroni 1991).

My research was part of a larger International Silvicultural Project at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) that explored sustained utilization of these montane forests. The overall project focused on both ecological and silvicultural research. The former was aimed at gaining sufficient ecological understanding of the oak-bamboo forests to allow its manipulation for sustainable management. The latter applied this ecological knowledge in experiments that analyzed forest response to selective logging coupled with silvicultural treatments.

I started my study on the dynamics of the primary oak-bamboo forests in 1987. My research focused solely on ecological questions (with no silvicultural manipulation) and was designed to include long-term monitoring of gap-phase and tree population dynamics. To date, some conclusive results have emerged, but further monitoring of the forest through re-census in later years will be required before the general principles of the dynamics of these oak-bamboo forests can be fully developed.

The primary objective of my study was to test the effect of slope gradient on the tree dynamics of this ecosystem. Slope gradient was chosen as the independent variable because most remaining primary forests in Costa Rica are on slopes (Sader and Joyce 1988) and because its effect on forests has not been well explored. In the long term, an understanding of the dynamics of pristine forests is crucial for developing sustainable management systems that mimic natural dynamics to the utmost extent feasible (Leibundgut 1982, Whitmore 1980, Oldeman 1990).

Hypothesis Testing

This study was conducted in a watershed that contained old-growth oak-bamboo forests on stable slopes that showed no evidence of large-scale natural disturbances such as landslides. Over the landscape, the forest was structurally homogeneous, with most patchiness occurring only at the scale of tree-fall gaps resulting from individual tree mortality. Physiognomically, the forest was tall, densely stocked, with complete crown closure in the overstory on both slopes and flats.

In this context, I hypothesized that different slope inclinations induce different conditions for forest development and create a pattern of the landscape in terms of differential local forest dynamics. My overall prediction was that forests on slopes are more dynamic than those growing on flat areas.

Because the term "forest dynamics" covers an array of processes, including growth, ingrowth, and mortality, the effect of slope on dynamics could not be tested directly. Therefore, by strong inference (Platt 1964), the overall hypothesis was broken down into a series of eight testable hypotheses with well-defined, measurable variables believed to be key elements of the oak-bamboo forest dynamics. These hypotheses were arranged sequentially in a "logical tree" (Fig. 1-1), with the following methodological approach in mind. At the level of each research hypothesis the corresponding null hypothesis was tested for rejection by statistical inference. The validity of the overall hypothesis was then assessed by a sequential evaluation of each of the individual hypothesis tests. Graphically, sequential rejection of the individual null hypotheses in favor of the research hypotheses would bring about a shift

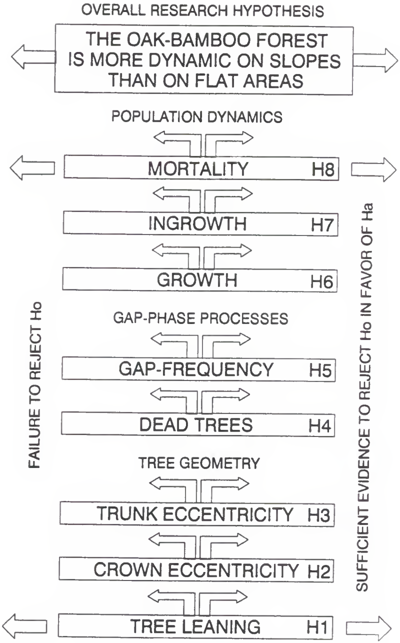


Fig. 1-1. "Logical tree" (Platt 1964) with sequential hypotheses subdivided into three sets (tree geometry, gap-phase processes, and tree population dynamics) before testing. Sequential rejection of the null hypotheses would gradually shift the logical tree to the right, providing supportive evidence for the overall hypothesis.

to the right of the logical tree (Fig. 1-1), providing supportive inductive evidence that forests on slopes are more dynamic than those on flat areas. In this approach, the weighting of each hypothesis in the search for an emergent conclusion is subjective and assumptions underlying the decision making process need to be evaluated with care.

The eight hypotheses were grouped into three sets which dealt with the effects of slope on tree geometry, gap-phase processes, and tree population dynamics (Fig. 1-1).

Tree Geometry

H_1 and H_2: Trees display down-slope leaning (H_1) and crown eccentricity (H_2) which correlate positively with slope angle regardless of aspect. Rejection of the corresponding null hypotheses would support the idea that slopes may have a negative effect on tree stability and may ultimately enhance tree-fall probability.

H_3: As a corollary to H_1 and H_2, trees on slopes display non-circular trunk cross-sections with longest diameter in down-slope direction. Rejection of the corresponding null hypothesis would strongly suggest the existence of costly reaction wood induced by a bending moment and provide further evidence of tree leaning and crown eccentricity on slopes. However, efficient allocation of reaction wood could also offset tendencies toward the expected greater tree-fall on slope.

Gap-phase Processes

H_4: The number of dead trees on the forest floor correlates positively with slope gradient. Rejection of the corresponding null hypothesis would support the postulate of increased tree-fall on slopes (assuming equal decay rates regardless of topography).

H_5: Gap area is greater on slopes. Rejection of the corresponding null hypothesis would suggest that forests on slopes are more likely to have more open canopies and consequently be more subject to tree fall.

Tree Population Dynamics

H_6: Relative growth rate (diameter) of trees is accentuated on slopes. Rejection of the corresponding null hypothesis would strongly suggest that stand turn-over is higher on slopes.

H_7: As a corollary to H_6, the number of trees growing into the smallest-measured diameter class (10 cm dbh) is higher on slopes.

H_8: Tree mortality rate is higher on slopes. Rejection of the corresponding null hypotheses to H_7 and H_8 would further support the faster forest growth and turn-over on slopes.

A sequential rejection of these null hypotheses would provide strong evidence to support the existence of more dynamic forests on steeper slopes.

The test of these hypotheses required long-term, large-scale monitoring of the forest, best achieved by means of a grid of permanent plots. As a result of the compositional and structural homogeneity of the oak-bamboo forest, coupled with the absence of large-scale disturbance, a plot size of 1 ha was estimated to be sufficiently large to include both forest matrix and gaps.

The study on gap-phase processes including hypotheses H_4 and H_5 is incomplete, but preliminary results are briefly discussed in the concluding chapter. This dissertation contains tests of hypotheses concerning tree geometry and population dynamics (H_1, H_2, H_3, H_6, and H_7).

CHAPTER 2
PHYSICAL SETTING OF STUDY AREA

Geography

Fieldwork for this study was conducted in a 20 km^2 area of oak-bamboo forest in the Cordillera de Talamanca, Costa Rica. The site is located near the continental divide in the upper Rio Macho Atlantic watershed at an elevation ranging from 2650 to 2850 m. It lies adjacent to the Pan American Highway northeast of the hamlet Villa Mills, 98 km from San Jose. Villa Mills is situated at the southern border of the Department of Cartago at 9°33' N latitude and 83°43' W longitude. On the 1:50000 topographic map "Cuericí" (IGN-CR 1955) Villa Mills is found at coordinates of the Military Grid Reference System (TM 1967) 390,000 m N and 495,000 m E. The study area lies within the polygon given by the parallel 393,000 m N, Quebrada Agua Negra, the continental divide, the Pan American Highway, and the Río Angeles (Fig. 2-1).

In Costa Rica, tropical montane oak-bamboo forest is largely confined to continuous tracts at elevations above 2000 m in the Cordillera de Talamanca (Blaser 1987, Orozco 1991). This range is the northwest-southeast mountainous axis of the country south of the Valle Central and extends

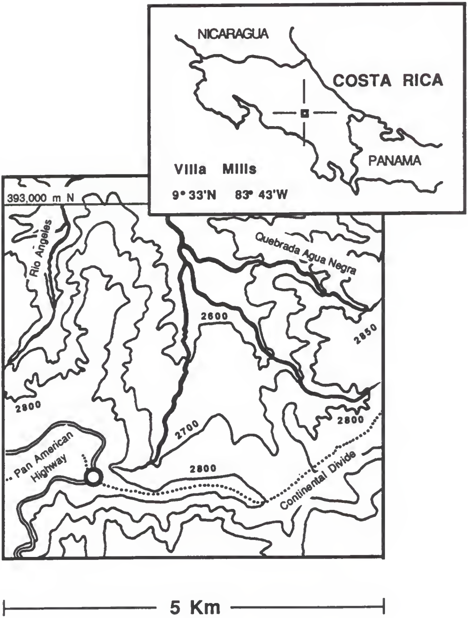


Fig. 2-1. Study area, upper Rio Macho watershed, Cordillera de Talamanca, Costa Rica. (o) The hamlet Villa Mills. (......) The Continental Divide.

from Cartago 300 km southeast into Panama. The Cordillera de Talamanca forms the continental divide and is composed of several separate massifs with elevations above 3000 m.

Geology and Geomorphology

Formed in the Cenozoic era, the Cordillera de Talamanca is a relatively young mountain chain. Its highest massif (Mt. Chirripó, 3820 m) is an upland plateau with Paramo vegetation and emergent igneous rock outcrops denuded of vegetation. It is bounded by steep forested slopes that are more abrupt on the Pacific than on the Atlantic side. The Talamanca Range is characterized by elongated crests with rugged ridges and long straight slopes representing angular, recent landforms.

The Cordillera de Talamanca contains no Paleozoic rocks. It is built from Tertiary marine sediments, intrusive igneous bodies, volcanic breccia, and metamorphic rocks found in intricate spatial arrangements (Weyl 1961, 1980). Its complex geology derives from the tectonics of converging plates in Central America. Malfait and Dinkelman (1972), Ladd (1976), Seyfried (1986), Seyfried and Sprechmann (1986), and Seyfried et al. (1987) have outlined Central America's geological history in detail. To summarize, during Late Triassic-Early Jurassic periods, North America and South America-Africa began to rift and the Gulf of Mexico formed. During these periods, a volcanicmagmatic arc developed along the Pacific margin of North America and South America-Africa, maintaining a land-bridge between these continents that is believed to have persisted until the Late Jurassic. During the Early Cretaceous, as the separation between South America and Africa began, a deep ocean basin divided North America from South America, giving rise to the proto-Caribbean sea.

In the Early Tertiary, a substantial reorganization of plates took place in the Caribbean region, bringing about increased volcanic and orogenic activity in Middle America. At the same time, a land mass grew at the western edge of the converging plate boundary of the recently formed Caribbean Plate as a complex volcanic arc-trench system. In the Middle and Late Tertiary period, the continentalization of the island arc of Central America was brought about by the subduction complex of the Caribbean and Coco Plates. In southern Central America, the subduction generated uplifting of marine sediments, plutonic intrusion, and strong volcanism. In addition, the northwesterly motion of South America decreased its disjunction from North America, arched and compressed Central America in Panama and Costa Rica, and formed the land-bridge in the Pliocene. The formation of the isthmus between North and South America and the creation of montane habitats in Central America have important biogeographic implications in facilitating long distance latitudinal migration of montane-adapted taxa (Flenley 1979, Coney 1982, Rich and Rich 1983).

In Costa Rica, the orogenic uplifting of the Cordillera de Talamanca began in the Oligocene and ended in the Miocene (Weyl 1957, 1961). The bedrocks are marine sediments from the Tertiary period and igneous rocks (Weyl 1961, DGMP-CR 1968). Plutonic intrusions and volcanic eruptions took place during the orogeny of the Cordillera but ceased in the Miocene (Weyl 1957, 1961). The Pliocene was an epoch of rhexistasy (geological interval with predominant erosional processes) during which erosion and deposition shaped the actual Cordillera, thereby denuding plutonic rock outcrops and creating undifferentiated sediment fans. In contrast to the northerly mountain range of Costa Rica, the Cordillera de Talamanca had no Quaternary volcanism (Weyl 1957, 1961, 1980). During the Pleistocene, glaciation of the Chirripó massif took place and relief features were subject to intensive alterations (Weyl 1961, Barquero and Ellenberg 1986) that caused a smoothing of the landscape contours on the plateau. Judged by the freshness of forms, Hastenrath (1973) estimates the age of the glaciation to be equivalent to Wuerm-Wisconsin (15,000 B.C.).

In recent time, frequent seismic activities such as the July 3, 1983, earthquake at Buenavista de Pérez Zeledón (epicenter near the study area) provide evidence of interplate neo-tectonic mobility (Madrigal 1977, Fischer

1980, Boschini et al. 1988). Earthquakes like these trigger landslides over extensive areas, accelerating geomorphological processes and shaping forest dynamics at the landscape level as large forest tracts are set back into earlier successional stages (Garwood et al. 1979). In the upper Rio Macho watershed, however, no signs of earthquake-caused landslides are present, indicating that the slopes are stable in spite of their steepness. In fact, the April 22, 1991, tremor near Puerto Limón (Richter scale 7.4) and its aftershocks in the Cordillera de Talamanca did not induce any rapid mass movement within the studied watershed. Geomorphological disturbances, mainly confined to stream bank slumps, do not create large forest openings as in other parts of the Cordillera (e.g., landslide prone Pacific slopes of the Cerro Cuericí; IGN-CR 1955).

The study area is covered by relatively homogeneous forests and includes slopes inclined 0° to 45° inclination. The core area contains a moderately northward inclined (0° to 10°) area of 300 ha bordered by two converging creeks. This relatively flat area, uncommon in the Cordillera (Ginneken and Calderón 1978), is surrounded by intermediate and steep mountain flanks that have slopes predominantly facing east or west. The drainage system has a dendritic pattern of first-order streams indicating the lithological uniformity of the upper Rio Macho watershed (Faniran and Jeje 1983). Its valleys are V-shaped with angular landforms, containing slopes with well-defined rectilinear segments, the result of parallel retreat stream erosion (Finlayson and Statham 1980). These geomorphic features suggest no past glacial activity. This is in concordance with Weyl (1956a, 1956b), Hastenrath (1973), and Barquero and Ellenberg (1986), who report Pleistocene snow line and glaciation limits in the Chirripó massif only at elevations above 3400 m. Consequently, the enigmatic presence of several striated boulders in the study area, interpretable as erratic blocks, must be explained as the deposition of Quaternary solifluction.

In the study site, the identification of rocks is difficult, as bedrock outcrops are scarce. Weyl (1957), however, has provided detailed geological observations from adjacent road cuts. He identified undifferentiated rocks of marine sediments intermingled with igneous rocks, breccia, and amorphous metamorphic rocks from Middle Tertiary time, and he also reported the occurrence of breccia-conglomerate, quartz-andesite, granite, gabbros, and thick volcanic ash layers (Weyl 1957, 1961, 1980).

Soils

Volcanic ash deposits are widespread and abundant throughout the western part of the Cordillera de Talamanca and are a very important parent material for soils of the region (Pérez et al. 1978). Since volcanism ceased in the

Miocene, these ash deposits are believed to stem from Quaternary volcanic activities of the adjacent Cordillera Central. Therefore, the autochthonous Tertiary soil parent materials of the Cordillera de Talamanca were repeatedly rejuvenated by external ash falls.

The ten soil pits (3 to 4 m deep) that I excavated within the study site revealed deep, ash-derived regolith with unconsolidated debris and weathered breccia. Increased overburden pressure made additional auger drilling at the bottom of the pits unfeasible and prevented reaching bedrock, even on slopes.

As expected in a montane forest, the soils of the study area display substantial organic horizons with characterisic root mats. Blaser (1987) measured several soil parameters with the help of soil technicians from the Centro Agrónomico de Investigación y Enseñanza (CATIE, Turrialba, Costa Rica). At 30 cm, the soils had less than 25% soil carbon, bulk density below 0.9 Mg m^{-3}, extractable aluminum of approximately 25 g kg^{-1}, phosphate retention above 90%, and a sand fraction dominated by volcanic glass. The soils qualify as Andisols (USDA 1990).

Blaser (1987) analyzed soil from 8 pits in the relatively flat part of the study area and found a predominance of Dystrandepts (Hapludands) and more sporadically distributed Placandepts (Placudands). The pH values (NaF 2 min) varied from 3.5 to 4.5 in the first 10 cm of the A horizon and stabilized at 30 cm with values from 4.5 to 5. Sand, silt, and clay comprised 75%, 15%, and 10%, respectively, of the B horizon of the Dystrandept (Hapludands) and 70%, 5%, and 25% of the B horizon of the Placandept (Placudands). Bulk density in the B horizon (15 to 50 cm) was approximately 0.6 Mg m^{-3}. Organic carbon content was approximately 20% in the A horizon and 8% in the B horizon. Phosphorous retention was 7 to 45 mg 100 g^{-1} in the top 15 cm and decreased to 2 to 5 mg 100 g^{-1} at 50 cm. These properties are characteristic of Typic Hapludands and Typic Placudands (USDA 1990). In general, the study area is dominated by Hapludands, with Placudands confined to one part of the flat area.

Soils were surprisingly deep on slopes, as I established from measurements carried out by driving a 150 cm metal bar into the soil at 60 systematically determined locations per hectare, over 21 hectares. Penetration was impeded by rocks at very few locations only. The transition from soil to ash regolith seemed more abrupt on slopes than on flats, where it was difficult to detect. Drainage on slopes was extremely good, attested to by the fast drainage of the deep soil pits I observed during periods of substantial rainfall.

I encountered sporadic fine roots down into the ash regolith at depths below 3.5 meters. In general, however, fine roots were confined to the A horizon and particularly to the thick organic mat that is characteristic of these montane forests. Fine roots did not usually penetrate the characteristic hardpan of the Placudands.

Climate

In Costa Rica, maximum daily radiation occurs when the sun passes directly overhead during May and September. The intertropical convergence zone (ITCZ) follows the sun path at its zenith with a lag of two months, reaching its farthest north latitude of 12° in August (Coen 1983). At the study site, this pattern generates a well-defined rainy season from late April to mid-December, followed by a dry season.

In Villa Mills, the average annual precipitation is 2800 mm (Blaser 1987). The curve of monthly average rainfall during the rainy season is slightly bimodal, interrupted in July or August by a poorly defined, short dry season, the "Veranillo de San Juan," which is associated with the most northerly extent of the ITCZ (Coen 1983).

The distribution of precipitation is strongly influenced by episodes of continuous rainfall that may persist several days. Such "temporales" result from air masses moving inland from either the east or west and produce orographic precipitation on the Atlantic and Pacific slopes, respectively (Coen 1983). The Atlantic temporales, called "nortes," are caused by cold fronts that penetrate the tropics during the early northern winter. Pacific temporales occur during strong tropical depressions in the Caribbean Sea, reversing trade wind patterns and bringing about rain on the western slopes of the mountains (Hastenrath 1966, Coen 1983). Because the study site verges on the continental divide, the area is affected by temporales from both the Atlantic and Pacific. In Villa Mills, the former tend to bring about rainy days during the beginning of the long dry season, whereas the latter cause strong rains and winds in October and November.

The altitudinal and topographic configurations of the study area also bring about some site-specific rainfall characteristics. The lower Río Macho basin, which lies at approximately 1000 m elevation, is fully exposed to the ascending northeasterly trade winds and receives the country's maximum annual rainfall of approximately 6000 mm. In contrast, the upper Río Macho watershed, which lies at 3000 m elevation, receives air that has dried as the result of heavy orographic precipitation on the west flanks of the Cordillera, bringing about a Pacific type of rainfall distribution in Villa Mills (Holdridge et al. 1971).

This precipitation regime is accentuated by the screening effect of the Cerro Cuericí. This peak is located to the east and shelters the study area from northeasterly trade winds. At Cerro Cuericí, ascending air currents from the Atlantic are blocked and channeled southward, crossing the mountains through a pass at lower elevations. This phenomenon is especially noticeable during the dry season, when trade winds are most intense (Coen 1983). On the Pacific side above San Isidro del General, descending winds produce a vertical vortex bringing about local south-westerly ground winds that reach the study site at the continental divide. Such winds often bring cloudiness sometimes associated with drizzling rains in the afternoon during the dry season.

The temperature data reflect the montane character of the study site. In Villa Mills, the average temperature of the warmest month, May (12.4° C), is roughly 3° C warmer than the coolest month, January (9.6° C). In contrast, the diurnal variation is high and can exceed 20° C in January or February. During these months, daily averages may reach a maximum of 18° C and a minimum of 2° C. Absolute minimums reach values of -2° to -3° C in January, February, and March. During the rainy season diurnal variation (approximately 10° C) is less pronounced.

Typical dry season weather consists of a morning with clear skies, relative humidity of 75%, and 2° C temperature. By midday, fog moves in and temperatures rise to 18° C; afternoons are cloudy with 90% humidity, slightly cooler temperatures, and occasional drizzling rain. During the wet season, high-altitude clouds create overcast conditions in the early morning, with average temperatures of 7° C. By mid-morning, clouds and fog start moving in from the northeast and by midday, temperatures increase slightly and rain frequently occurs. There is usually rain in the afternoon and temperatures drop slightly to about 9° C. The humidity remains above 95% for the whole day.

Vegetation and Flora

According to Holdridge et al. (1971), the climatic environment in Villa Mills defines the potential natural vegetation of the study area as Tropical Montane Rain Forest. Physiognomically, the oak-bamboo forest of the upper Rio Macho watershed is a tall, densely stocked, closed-canopy, evergreen, old-growth forest. It is dominated by two oaks, *Quercus copeyensis* Corn. Mueller (copey oak in English, roble in Spanish) and *Quercus costaricensis* Liebmann (Costa Rican oak in English, encino in Spanish), and has dense *Chusquea* spp. bamboo thickets in the understory. These forests were described with amazement by foresters travelling with the Latin American Forest Resources Project of the United States Department of Agriculture, Forest Service, in 1943, while the Pan American Highway was under construction (Barbour 1943, Bevan 1943, Merker et al. 1943, Dayton 1944). The most remarkable feature of the oak-bamboo forest is its relatively great dominant height (35 m; Blaser 1987) that contrasts markedly with the low stature of most montane forests (e.g., Grubb 1977, Tanner et al. 1992).

For a tropical montane vegetation formation, the oak-bamboo forest is floristically rich (Kappelle 1989). Its composition is the result of both latitudinal immigration following long distance dispersal from both the northern and southern hemispheres, and altitudinal invasion by adaptation from lowland taxa (Van der Hammen and Cleef 1983). In the late Pliocene, the Cordillera de Talamanca was high enough to provide habitats and corridors for montane-adapted plants (Raven and Axelrod 1974, Raven 1975), and *Quercus* spp. and *Alnus* spp. migrated southward from the Holarctic region into the neotropical mountains. At present, oak forests are found as far south as Colombia and northern Ecuador (Vega 1966). Palynological analysis from peat bog cores in the Talamanca Range indicate the presence of *Quercus costaricensis* and *Q. copeyensis*, as well as *Chusquea* bamboo in the late Pleistocene (Martin 1964, Cleef et al. 1990). *Weinmannia*, *Podocarpus*, *Drimys* and *Ilex*, all trees found in the study site, are of Austral-antarctic origin. In contrast, *Styrax*, *Clethra* and *Dicksonia* are of tropical origin (Raven and Axelrod 1974, Van der Hammen 1974, Van der Hammen and Cleef 1983, Smith and Cleef 1988, Van der Hammen 1989).

Kappelle et al. (1989) conducted a phytosociological study of the western part of the Cordillera de Talamanca and described four oak forest communities. In ascending altitudinal order the forest types are: 1) *Q. seemannii* - *Q. copeyensis*, 2) *Geonoma hoffmanniana* - *Q. copeyensis*, 3) *Q. costaricensis* - *Q. copeyensis*, 4) *Myrsine pittieri* - *Q. costaricensis*. The 22 vegetational relevés contained a total of ten sociological groups and 190 species, including 107 phanerogamic species. The oak-forest encountered in the study is a *Q. costaricensis* - *Q. copeyensis* forest association and occurs extensively between 2550 and 2950 m.

For the *Q. costaricensis* - *Q. copeyensis* forest type in Villa Mills, Kapelle et al. (1989) recognized five structural layers. Blaser (1987), however, reported six strata, including emergents that are taller than 45 m (reaching a maximum of 56 m). Holdridge et al. (1971) reported 37 tree species, Blaser (1987) reported 42 species, and within the sample plots (21 ha), I identified 46 tree species. Kappelle et al. (1991) provide a list of 483 native woody species from the high (≥ 2000 m) areas of the Cordillera de Talamanca.

In general, the canopy in the study area averages 30 to 40 m in height and is dominated by *Q. copeyensis* and the slightly smaller *Q. costaricensis*. *Weinmannia pinnata* L., *Ocotea austinii* A., and the two gymnosperms *Prumnopitys standleyi* Laubenf. and *Podocarpus macrostachyus* Parl., are codominant in the upper stratum. The sub-canopy layer, with average height of 25 m, includes trees such as *Styrax* *argenteus* Presl. and *Drimys granadensis* Laubenf. The understory layer is dominated by three newly described bamboo species (*Chusquea tomentosa* W.& C., *C. subtilis* W.& C., and *C. talamancensis* W.& C.; Widmer and Clark 1991) and shrubs belonging to the Ericaceae, Rubiaceae, Myrsinaceae, Melastomataceae, and Onagraceae families. The herb layer is dominated by ferns and aroids. Bromeliads, ferns, and orchids are the abundant vascular epiphytes; *Clusia* and *Dendropanax* are common hemiepiphytes.

CHAPTER 3
TREE LEANING AND CROWN ECCENTRICITY IN RELATION TO SLOPE

Introduction

Competition for light was presumably a major selection pressure that favored evolution of the tree habit (e.g., Niklas and Kechner 1984, King 1990). In addition to orthotropic bole extension of trees, plagiotropic crown development was also attained, a trait especially well developed in dicotyledonous angiosperms. The capability to achieve lateral branching and crown expansion is hypothesized to optimize light-capture efficiency and is largely dependent on the inherent architectural plan of tree species (Hallé et al. 1978, Tomlinson 1987). In a closed-canopy forest, however, competition brings about a variety of crown forms even within a given architectural model, as many angiosperms respond to canopy light environments with considerable phenotypic plasticity (Fisher 1984, Fisher 1986, Tomlinson 1987).

The simplest model is to assume that light and gravity lead to an overall negative geotropic growth response of trees and that the mean orientation of all crown eccentricities resulting from competition is random. The assumptions of vertical trees and symmetrical crowns in a stand, based perhaps upon attractive ideas of optimal design (Maynard Smith 1978, Horn 1979), only make intuitive sense in homogenous forests on level ground where trees are not disturbed by directional influences such as wind or proximity to forest edges.

On slopes, light fields are asymmetric (Phipps 1974, Givnish 1986) and gravity and light, the two main environmental stimuli that induce directional growth of trees (Hart 1988), can be regarded as separate vectors. Consequently, geoplagiotropic (oblique to gravity) growth responses, that vary with steepness of terrain, should result. Furthermore, most trees on slopes are shaded by overtopping crowns of up-slope neighbors, which should induce down-slope crown extension. In forests primarily dominated by phototropic species with high phenotypic plasticity (e.g., broadleaf forests), down-slope tree leaning and crown eccentricity should result and these would likely lead to higher-than-average rates of treefall.

Tree leaning on slopes is seldom explained in the forest ecology literature as a phototropic response to asymmetric light fields. This is not surprising, as most knowledge of tree development on slopes derives from temperate zone forests dominated by gymnosperms, most of which are distinctly geotropic species that grow vertically under most circumstances (Smith 1962). Moreover, down-slope tree inclination is often related to snow pressure

(Leibundgut 1984) or soil movement (Scurfield 1973, Alestalo 1971). In geology and geomorphology textbooks, trees showing down-slope curving trunks associated with soil creep and solifluction are often reported as faits accomplis (Sharp 1938, Bloom 1969, Faniran and Jeje 1983). Imada (1980) quantified tree inclination on slopes and reported more down-slope tree inclination of broadleaf species than of conifers. He attributed the overall tree tilting to soil erosion, leaving the differential response of the two phylogenic groups unaddressed.

Nevertheless, Parizek and Woodruff (1957) questioned the notion that soil creep is the sole process inducing tree deformation, and Phipps (1974), working in eastern U.S. deciduous forests, described tilting and curvature of trunks as geotropic and phototropic responses to physical and physiological conditions mostly unrelated to soil creep. Moreover, red alder in the Pacific Northwest is known to respond to competition by leaning toward open areas (Willits et al. 1990). In a more quantitative study, Swanson et al. (1989) explored the relationship between stem deformation and soil mass-movement in a western U.S. coniferous forest and defined tree form classes as indicators of earthflow velocities. In a montane forest in Peru, Young and León (1990) analyzed stem curvature of small woody plants and attributed the observed down-slope deformation to litter creep and branch fall affecting young plants confined to certain size classes only.

The eccentric development of crowns as a response to oblique light is widely reported in the silvicultural literature (Trimble and Tryon 1966). Hibbs (1982), Runkle and Yetter (1987), and Frelich and Martin (1988) examined crown expansion into treefall gaps, while Young and Hubbell (1991) explored the implications of such a pattern on treefall and gap dynamics. However, geoplagiotropic tree growth response and crown eccentricity induced by asymmetric light on slopes is not widely reported in the literature, and there is need for further exploration of this question in broadleaf forests where snow pressure and rapid soil creep are not prominent factors.

The objectives of my study were to quantify tree inclination, crown eccentricity and non-circularity of stem cross-sections, to explore the underlying causal processes responsible, and to discuss the implications for dynamics of the montane oak-bamboo forest in Costa Rica. The study was conducted in three phases. First, an initial assessment of canopy tree inclination and crown eccentricity on steep slopes was carried out on sites of disparate aspects to evaluate the potential effect of directional trade-winds on tree leaning and crown eccentricity. Second, canopy tree inclination and crown eccentricity as well as sub-canopy tree inclination were quantified at sites having different slope angles of determined aspect, including control sites with no slopes (i.e., flat topography). Finally, soil creep and inclination of small trees and seedlings were measured to determine whether soil creep or asymmetric light is more likely to be the underlying process behind this hypothesized inclination pattern. Within this context, the following main hypotheses were formulated:

1) : canopy trees (diameter at breast height [dbh] ≥ 20 cm) on steep forested slopes (30° < slope < 40°) display down-slope stem inclination and crown eccentricity on all aspects independent of predominant trade-wind direction;

2) down-slope canopy tree (≥ 20 cm dbh) inclination, crown eccentricity and non-circular stem cross-section, as well as sub-canopy tree (10 to 20 cm dbh) inclination, correlate positively with slope inclination;

3) small trees and saplings (1 m ≤ height ≤ 5 m) and seedlings (0.10 m ≤ height ≤ 0.50 m) exhibit down-slope stem inclination on steep slopes; and,

4) down-slope mass movement (creep) on slopes does not produce sufficient soil shearing to explain tree inclination.

Methods

Study Area

The field research was conducted in the oak-bamboo forest described in Chapter 2. This forest constitutes a suitable system in both structure and composition for testing hypotheses concerning plagiogeotropic growth response of trees on slopes. At a latitude of approximately 10° N, it lies well outside the range of snowfall that could bias the findings on tree inclination, despite its high elevation of 3000 m. Furthermore, the oak-bamboo forest includes large homogeneous tracts of old-growth forest on rugged terrain that do not display evidence of severe large scale disturbances, such as hurricane damage and landslides. Moreover, evergreen oaks of the genus Quercus are believed to display a marked degree of orthotropic-plagiotropic differentiation between trunk and branch (Hallé et al. 1978), and have considerable phenotypic crown plasticity in competitive light environments (Oliver 1975).

Sampling Design

Canopy tree response to aspect

To test tree inclination and crown eccentricity as functions of aspect (hypothesis 1), data were collected on nine sites on steep slopes that covered the complete range of slope directions encountered in the study area. First, to allocate potential sites, nine strata with differing aspects were highlighted on a 1:50000 topographic map (IGN-CR 1955), following criteria related to slope angle (30° to 40°), surface configuration (straight slope segments excluding the convexity of ridges and the concavity of lower slopes), and altitude (2800 to 3000 m). Second, sites were selected randomly from those areas by means of an overlaid grid, and then located in the forest using a compass and hip chain. Third, at each site, two perpendicular 50 m transects were staked temporarily and 30 canopy trees (dbh ≥ 20 cm) were selected by random coordinates. Consequently, at each site data from 30 trees (sample units) were collected over an area sufficiently large (2500 m^2) to meet the assumption of independence of errors among sample units and to allow statistical comparison among sites. In addition, the ratio of crown area (approximately 64 m^2 per tree) to sample area (2500 m^2) was negligibly small (0.025), further reducing potential for violation of the independence of errors (Green 1979).

Given the singularity of the design of this study, caution should be exercised in the interpretation of its results. To maximize the ratio of information gained to effort expended, and due to topographical constraints, the nine "treatments" (i.e., aspect) were not strictly replicated. As a consequence, potential differences between sites may not necessarily reflect true "treatment" effects. I felt confident, however, that if trees on sites with similar aspects displayed similar responses, the hypothesis of a directional pattern would be strongly supported.

Canopy and sub-canopy tree response to slope inclination

To test for positive correlations of tree leaning, crown eccentricity, and non-circular stem cross-section with slope inclination (hypothesis 2), data were collected from permanent 1-ha sample plots initially laid out for a long-term study of the effect of slopes on forest dynamics (Chapter 4). Three ranges of slope inclination were defined as main treatments: flat (0° to 10°), intermediate (25° to 30°), and steep (30° to 40°). Each treatment was replicated five times (15 sample units). Aspect (west-facing) and soil type (Hapludand) were kept constant. To test for covariability, the intermediate slope treatment was repeated three times on a contrasting aspect (east-facing), and the flat treatment was repeated three times on a different soil type (Placudand). These secondary treatments are hereafter referred to as "east aspect" and "Placudand". A total of 21 1-ha plots resulted from the overall sample design.

The potential location of plots was initially defined on a 1:50000 map following a stratified random process. The study area was broken up into five strata incorporating the three slope angles, two aspects, and two soil types. Based on ground reconnaissance, creeks with unrepresentatively steep banks were excluded. Plot corners were then randomly selected on the map and their location in the field was determined with compass and hip chain. One hectare plots were subdivided and staked into subplots of 20 x 25 m (500 m^2).

Within each plot, all trees with dbh ≥ 10 cm were tagged for the tree population dynamics study (Chapter 4). From this population, 61 to 65 canopy trees (≥ 20 cm dbh) per plot were randomly selected for sampling. Total sample size over the 21 plots was 1328 trees. Furthermore, all sub-canopy trees (10 to 20 cm dbh, large pole wood) were selected from five random subplots within each plot, yielding a total of 1107 trees. The sampling design for sub-canopy trees (10 to 20 cm dbh) was based on area rather than number of trees, resulting in uneven sample sizes and spatial segregation. These slight statistical disadvantages were greatly offset by logistical advantages.

Small tree and seedling response to slope inclination

Data to test small tree (including saplings) and seedling stem inclination in relation to slope (hypothesis 3) were based on randomly located transects on steep slopes. Small trees and saplings (1 to 5 m tall) were sampled including species of the mature forest only. Ten 50 m line transects on steep slopes were established and 30 trees were chosen along each transect by selecting the nearest tree to each of 30 randomly chosen points.

Seedlings ranging from 0.1 to 0.5 m tall were sampled from a population of even-aged oaks from the 1989 mast (recognized by their annual pseudo-whorls). In contrast to the small-tree study, a control area on flat ground (< 2° slope) was established for the seedling study. Within areas of steep slope and flat ground of approximately one ha each, three 50 m line transects were randomly located and 25 seedlings were selected along each transect as described above.

Soil creep

Soil creep (hypothesis 4) on steep slopes was monitored over a two year period by means of 12 modified Young pits (Finlayson and Statham 1980). A 1.3 cm diameter guiding tube was driven into the soil perpendicular to the slope until, at a depth of approximately 2.5 m, overburden pressure, hard pans, or parent material impeded further penetration. At each pit, approximately 80 solid aluminum cylinders (4 cm long by 1 cm diameter) were stacked into the guiding tube, which was subsequently removed. After two years, a large pit was carefully excavated adjacent to each column of cylinders to measure down-slope displacement due to soil shearing.

Data Measurements and Statistical Analysis

Basic measurements

In this study, species, diameter, height, slope angle and aspect were recorded in the following manner: 1) two voucher samples per species were identified in situ and later deposited in the herbarium at CATIE, Turrialba, Costa

Rica); 2) diameter of canopy and sub-canopy trees (dbh $\geq$ 10 cm) were measured at breast height (1.3 m), or above buttresses) with caliper to the nearest cm in both slope and cross-slope direction; 3) total tree height and height to crown base, the latter defined as the height to the lowest major branch excluding epicormic shoots, were measured with a hypsometer to the nearest 50 cm for both canopy and sub-canopy trees; tree height of small trees and saplings were measured to the nearest dm with a telescoping measuring rod; 4) local slope angle (β), was measured as the angle between the horizontal plane and the fall line (line connecting the tree base with the lowest terrain point encountered at 5 m away); 5) local aspect, defined as the azimuth angle to the normal of the slope at any given point, was measured in the field as the azimuth angle of the fall line direction. Vertical angles, as in slope angle, were measured with a clinometer, horizontal angles, as in aspect, with a compass to the nearest degree.

Tree leaning

Tree leaning in space is defined by two angles, tilt angle (Θ) and tilt direction (Φ). Tilt was defined as the angle of the tree axis (straight line from tree base to crown base) from the zenith and measured with clinometer to the nearest degree. Tilt direction was defined as the azimuth angle of the projected tree axis on the horizontal plane and measured with compass to the nearest degree.

In this study, angular measurements generated circular data on an interval scale that required the use of circular statistics. Angular data can be expressed as unit vectors on a circle with radius 1. The mean angle is obtained in a first-order analysis (Batschelet 1981), best explained with a vector diagram. Imagine a vector polygon formed by head to tail addition of unit vectors. The resultant vector of this polygon is the straight line from the tail of the first unit vector to the head of the last. The mean vector (R) of the unit vectors is obtained by dividing the magnitude of the resultant vector by the number of unit vectors of the polygon. The direction of R corresponds to the mean angle. The magnitude of R, which can have possible values ranging from 0 to 1, is a measure of concentration, because it varies inversely with the amount of dispersion in the original angular data. The mean vector of a perfectly grouped angular data set has magnitude 1. A similar second-order analysis is used to determine the mean of a set of vectors with magnitudes < 1 (Batschelet 1981), and is suited to generate the mean of means (average of various 'R's).

Tilt (Θ) and tilt direction (Φ) define tree leaning in space and together constitute a spherical data set expressed in polar coordinates (Fisher et al. 1987). For simplification, they were analyzed separately with circular statistics when appropriate. However, disjunct statistical analysis of tilt and tilt direction excludes the valuable interdependency of information between these variables on tree inclination contained in the data set as a whole. To avoid the loss of information, I also used an analytical approach based on both orthographic projection and equal-area projection (Lambert projection) of the spherical vectorial data (Mardia 1972, Fisher et al. 1987), discussed below.

Tilt direction. On the unit hemisphere (Fig. 3-1), the unit vector OP (OP = 1) is defined in polar coordinates by zenith angle Θ (tilt) and azimuth Φ (tilt direction). The orthographic (vertical) projection of the vector OP onto the X-Y plane is vector OP'. The direction of vector OP' remains azimuth Φ. The magnitude of vector OP' is sine Θ and assumes possible values ranging from 0 to 1. Vector OP' is a tilt direction vector that incorporates information on Θ through its magnitude. However, orthographic projections are useful primarily for displaying spherical data and were used only for that purpose in this study. For analysis, the densities of points P on the surface of the hemisphere needed to be preserved on the plane of projection and appropriate Lambert (equal-area) projections (Fisher et al. 1987) were used. For each tree data point, $0_LP'_L$ onto the X_L-Y_L plane (Fig. 3-1) was computed and utilized to calculate the weighted tilt direction mean over all trees by use of second-order analysis. This weighted mean is the

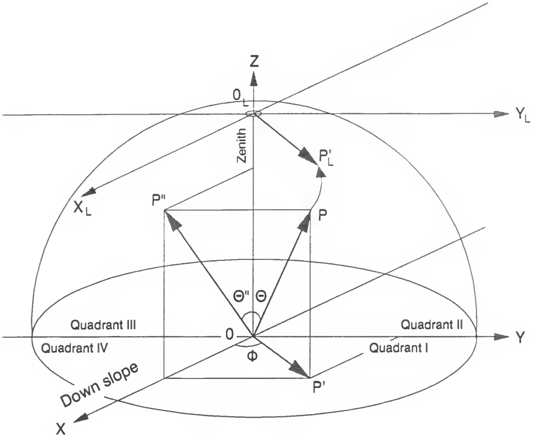


Fig. 3-1. Unit hemisphere with vector OP (unit vector of one data point) defined by zenith angle θ (tilt) and azimuth angle Φ (tilt direction). Vector OP' is the orthographic projection of OP onto the horizontal plane X-Y. Vector $O_LP'_L$ is the equal-area projection (Lambert projection) of OP onto the horizontal plane X_L-Y_L. Vector OP'' is the horizontal orthographic projection of OP onto the vertical plane X-Z. Note: The X-Z plane was set in the down-slope direction (i.e., θ is the difference between slope direction and tilt direction).

projected grand mean tilt-direction vector on the X_L-Y_L plane.

Tilt. Calculation of the mean tilt angle by first-order analysis provides no information on tilt direction, because tilted trees are distributed in space in an inverted cone. To relate tree inclination to tilt direction (and aspect), the component of the tilt angle θ onto the X-Z plane was calculated as θ'' (Fig. 3-1). On the unit hemisphere, the horizontal projection of the vector OP onto the X-Z plane is vector OP''. Note that the X-Z plane has been set in the average down-slope direction (first order mean of local slope directions), and that Φ is equivalent to the difference between slope direction and tilt direction. The zenith angle θ'' (projected tilt) of vector OP'' indicates the down-slope component of tilt angle when trees are leaning into quadrants I and IV. When trees are leaning into quadrants II and III, θ'' provides the up-slope component of tree tilt. The magnitude of vector OP'' is a function of Φ and can assume possible values from 0 to 1. Vector OP'' is a tilt vector that incorporates information on tilt direction through its magnitude. By use of the second-order analysis, the weighted tilt mean was obtained as a projected grand mean vector. This approach was used in orthographic projection for display and in equal-area projection for analysis.

Crown eccentricity

Down-slope crown eccentricity occurs when down-slope crown radii are significantly greater than up-slope radii. Crown radius was defined as the orthogonal projection of the distance between crown base to crown periphery onto the horizontal plane (verticality determined with crosswise clinometer readings), and was measured to the nearest dm in six directions (i.e., down-slope and up-slope, orientation of tree inclination along with its opposite, and cross-slope in both directions).

To account for differential crown size among trees, the null hypothesis

$$\frac{r_1}{r_1+r_2} - 0.5 = 0,$$

where r_1 and r_2 are opposite crown radii, was used for testing for down-slope crown eccentricity. Trees with partially broken crowns were included in the analysis, in contrast, snapped trees were deleted, as such trees provided no information on crown eccentricity.

Trunk eccentricity

In general, trunk eccentricity is defined as diameter perpendicular to the widest diameter, divided by the widest diameter (Husch et al. 1982, Biging and Wensel 1988). In analogy, down-slope trunk eccentricity was defined as diameter in slope direction (d_s), divided by diameter in cross-slope direction (d_{cs}). To test for the propensity of stem eccentricity in the down-slope direction, the following null hypothesis was used:

$$\frac{d_{cs}}{d_s} - 1 = 0.$$

Results

Canopy Tree Response to Aspect (Hypothesis 1)

The test of aspect effects on tree leaning and crown eccentricity was conducted on slopes ranging from 28° to 37°. Average slope of transects was established as the first-order mean of slope angles at bases of the trees in each transect.

Tree leaning

Of the 270 canopy trees (> 20 cm dbh) sampled, 87% displayed measurable deviation from vertical. Mean tilt of all trees, regardless of tilt direction, was 10°, and mean projected tilt ($\bar{\theta}''$) on the X-Z plane in the down-slope direction was 8.8°. The high ratio of mean projected tilt to mean tilt (0.88) indicates that inclined trees lean mostly in the down-slope direction. The circular standard deviations of mean tilt ($R_t = 0.91$) and mean projected tilt

(R_{pt} = 0.95) were expectedly small, as tilt data per se lie within a small possible range. Mean projected tilt angles ($\bar{\theta}''$) for each transect ranged from 3° to 17° (Fig. 3-2).

The frequency distribution (n = 270) of projected tilt by 2° classes (all transects pooled) showed pronounced skewness to the right, deviating significantly from normality (Shapiro-Wilk W statistic, p = 0.001, skewness = 2.9, mean 8.8°, median 5.4°; Fig. 3-3). These results illustrate the predominance of down-slope tilting. Overall tree leaning in space was distributed in a reverse ellipse-like cone with a down-slope inclined cone axis.

The average aspect of each site was determined as the first-order mean of the local slope directions measured at the tree bases (n = 30 per site). The resulting aspects were quite evenly distributed around the compass (Fig. 3-4, outer, dashed circle and dashed arrows). The magnitude of the mean aspect vector represents the terrain variability of the sample site, with perfectly planar sites having a magnitude of 1. Actual magnitudes ranged from 0.82 to 0.97, indicating low within-site micro-relief variability.
Mean tilt-direction by site was calculated using first-order means of all trees displaying tilt (n = 235) (Fig. 3-4, inner, solid circle and solid arrows). The circular-circular correlation showed a high directional agreement between the tilt direction and aspect vectors at all sites, with no outliers. A linear plot of the same data revealed a

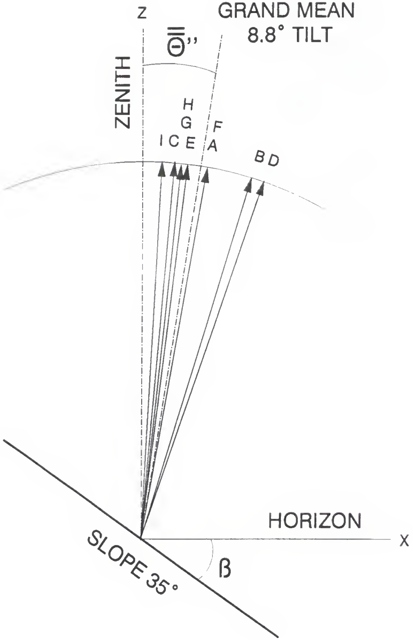


Fig. 3-2. Mean projected tilt angles ($\bar{\theta}''$) onto the X-Z plane for transect A to I (n = 30) and their grand mean (n = 270). Grand mean of projected tilt is 8.8° in the downslope direction.

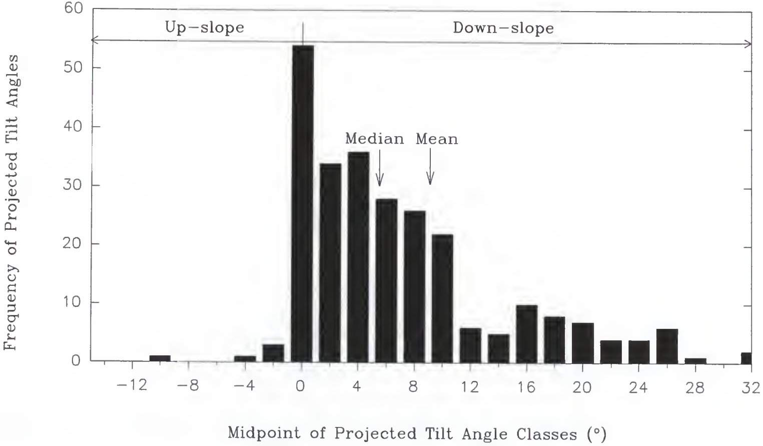


Fig. 3-3. Frequency distribution of projected tilt angles (θ'') for canopy trees onto the X-Z plane (down-slope) for all transects. Skewness = 2.9, mean projected tilt angle ($\bar{\theta}''$) = 8.8° and median = 5.4°.

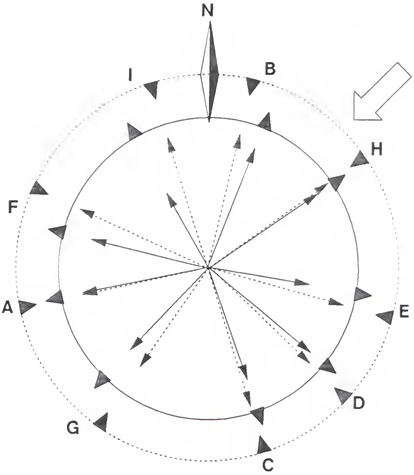


Fig. 3-4. Circular-circular correlation of tree tilt direction and slope aspect for all trees displaying tilt (n = 235). Solid vectors are first-order means of tilt-direction by site A to I. Dashed vectors are first-order means of aspect by site. Mean tilt directions are reported on the inner circle (solid), and aspect on the outer circle (dashed). Vectors (magnitude R between 0 and 1) are drawn to scale, with the inner circle set to a radius of 1. Arrow in north-east quadrant indicates the prevailing trade wind direction.

highly significant correlation between tilt-direction and aspect ($r^2 = 0.99$) (Fig. 3-5). Directional agreement between tilt direction and aspect is maintained around the compass, suggesting that tree leaning is not caused by any dominating directional factor unrelated to aspect. Magnitudes of the mean tilt direction vectors ranged from 0.59 to 0.90, indicating that tilt direction is markedly grouped around the mean but is more variable than aspect (i.e., had shorter vectors).

An ANOVA and subsequent Tukey's Multiple Range Test on projected tilt means showed differences among sites and revealed that sites could be grouped into three classes of differing tilt patterns. Sites B and D displayed significantly more tilt than sites C, E, G, H, and I, whereas sites A and F did not differ from either group (Fig. 3-2). These differences, however, do not correlate with any directional pattern on the compass (Fig. 3-4), and do not support the effect of directional trade-winds (or other possible directional factors unrelated to aspect) as the reason for tilting trees.

Crown eccentricity

Crown eccentricity was first tested for using the pooled crown radii data collected in both slope and tilt directions (n = 270 canopy trees). The null hypotheses of symmetric crown elongation in the direction of slope and in the direction of tree tilt were both rejected ($p = 0.0001$).

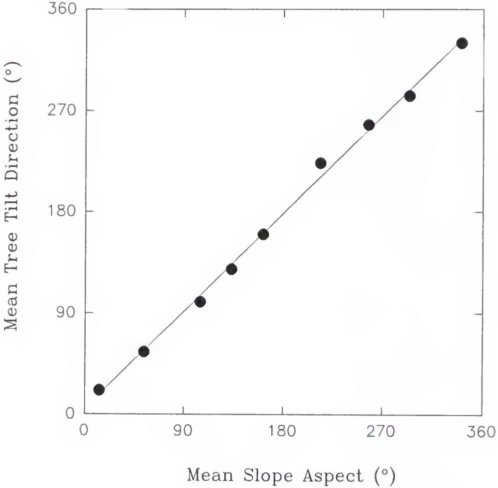


Fig. 3-5. Tree tilt direction as a function of slope aspect. Correlation coefficient, r^2, = 0.98.

On average, down-slope crown radii exceeded up-slope crown radii by 16%, and crown radii in the direction of tilt exceeded opposing crown radii by 22%. These findings suggest that crown eccentricity is driven by slope-related processes.

Crowns displayed significant down-slope eccentricity at all sites except H and I ($p = 0.058$ and $p = 0.095$). Because the seven sites where tree crowns displayed significant down-slope eccentricity were scattered throughout all four compass quadrants (Fig. 3-4), down-slope crown eccentricity is presumably independent of aspect. The lack of significance at sites H and I is probably due to high variance as a consequence of a small sample size.

Canopy and Sub-Canopy Tree Response to Slope Inclination (Hypothesis 2)

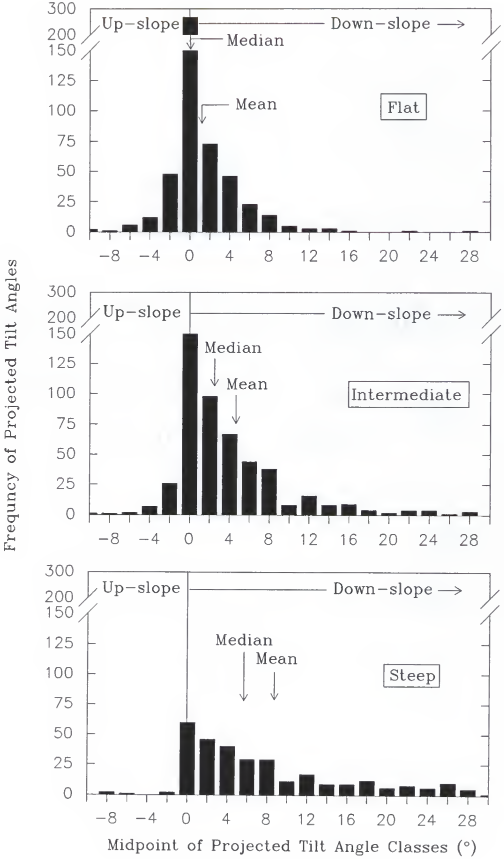
The next objective was to test the effect of slope on tree inclination, crown eccentricity, and non-circular stem cross-section using the permanent 1-ha plots. Average slope and aspect for each plot were established as the first-order means of slope angles and aspects measured at individual tree bases. Mean slope and aspect variability were low on steep and intermediate slopes, suggesting that the slopes were fairly straight with unbroken micro-relief. In contrast, the control plots in the "flat" area had relatively high slope and aspect variability. In fact, the control plots displayed moderately inclined terrain with average slopes ranging from 7.5° to 9.7° with uneven (rippled) micro-topography.

Tree leaning

The mean proportion of canopy trees (> 20 cm dbh) that displayed measurable deviation from vertical orientation increased with slope inclination (flat, 8 plots, 506 trees, 62%; intermediate, 8 plots, 507 trees, 80%; steep, 5 plots, 315 trees, 86%). Frequency distributions of projected tilt angles by 2° classes (pooled by the three basic slope treatments) showed an increased down-slope skewness from flat to steep sites, bringing about a shift of both means and median (Fig. 3-6). Means of projected tilt by treatments showed marked increase from flat to steep (Fig. 3-7).

A linear regression of square-root-transformed projected tilt angle means against slope angle by plot was highly significant ($p = 0.0001$, $r^2 = 0.85$; Fig. 3-8). Because of the skewness of the projected tilt angle data, a linear regression of square root-transformed projected tilt angle medians against slope angles was also calculated and found to be highly significant ($p = 0.0001$, $r^2 = 0.89$) (Fig. 3-9). Furthermore, the ratio of projected tilt angle to tilt angle was found to correlate positively with slope inclination ($p = 0.0001$, $r^2 = 0.78$; Fig. 3-10) supporting the dependence of down-slope leaning of trees on slope inclination.

Fig. 3-6. Frequency distributions of projected tilt angles (θ'') for canopy trees onto X-Z plane (down-slope) pooled over slope categories. Flat: mean ($\bar{\theta}''$) = 1.2°, median = 0°. Inter: mean ($\bar{\theta}''$) = 4.2°, median = 2.1°. Steep: mean ($\bar{\theta}''$) = 8.8°, median = 5.6°.


Frequncy of Projected Tilt Angles
Midpoint of Projected Tilt Angle Classes (°)
Up−slope
Down−slope ⟶
Median
Mean
Flat
Intermediate
Steep
300
200
150
125
100
75
50
25
0
−8
−4
0
4
8
12
16
20
24
28

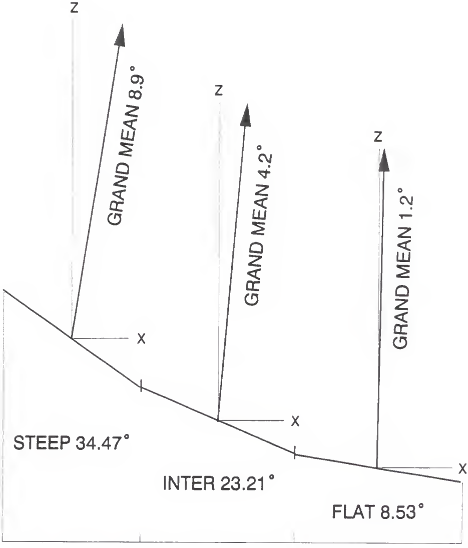


Fig. 3-7. Grand means of projected tilt of trees dbh ≥ 20 cm for flat (n = 480, 8 plots including flat Placudand), intermediate (n = 480, 8 plots including east aspect) and steep (n = 300, 5 plots).

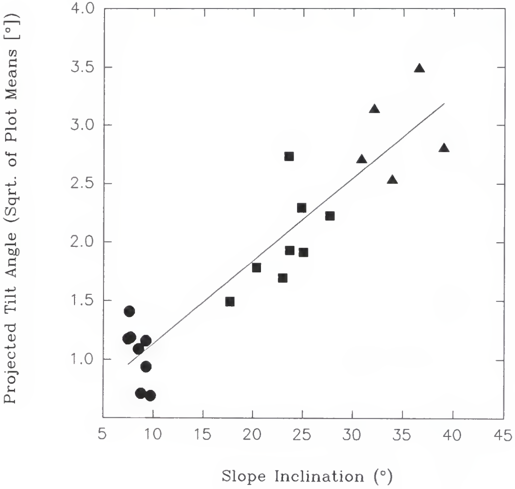


Fig. 3-8. Square root transformation of plot means of projected tilt angles as a function of slope inclination ($p = 0.0001$, $r^2 = 0.86$). Symbols indicate slope inclinations: ■ flat, ● intermediate, ▲ steep.

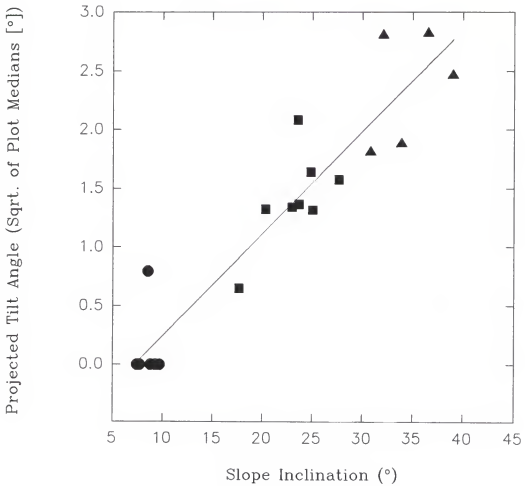


Fig. 3-9. Square root transformation of plot medians of projected tilt angles as a function of slope inclination ($p = 0.0001$, $r^2 = 0.89$). Symbols indicate slope inclinations: ▪ flat, • intermediate, ▲ steep.

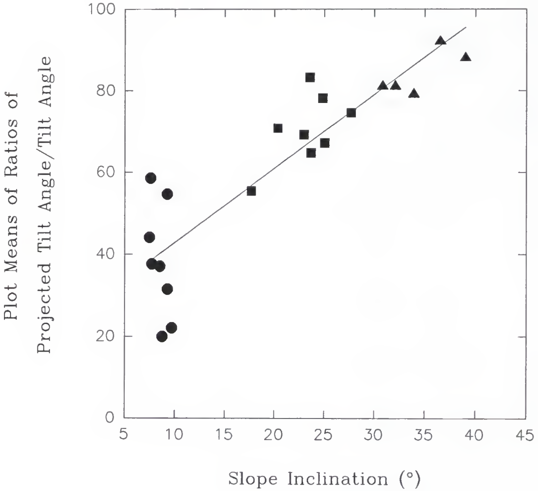


Fig. 3-10. Plot means of the ratio of projected tilt angle to tilt angle (θ''/θ) as a function of slope inclination ($p = 0.0001$, $r^2 = 0.78$). Symbols indicate slope inclinations: ■ flat, ● intermediate, ▲ steep.

On flatter areas, average tilt direction by plot, based only on trees displaying a measurable tilt, showed poor agreement with aspect. With increasing slope, however, average tilt direction and aspect showed increasing directional agreement, and circular dispersion decreased (vectors display larger magnitude; Fig. 3-11), further supporting down-slope inclination of trees.

Sub-canopy trees (10-20 cm dbh) showed a similar, slightly more accentuated leaning pattern than canopy trees. Frequency distribution of projected tilt angles by 2° classes displayed increasing skewness with slope inclination. Mean and median of down-slope projected tilt angles were 1.4° and 0° for control plots on flat areas (n = 480 trees), 4.9° and 2.4° for intermediate slopes (n = 405 trees) and 11.6° and 6.0° for steep slopes (n = 222 trees). Linear regression of square root-transformed plot means and medians were both positively correlated with slope ($p = 0.0001$, $r^2 = 0.70$, means; $p = 0.0001$, $r^2 = 74$, medians).

Crown eccentricity

Crown eccentricity was tested for using crown radii data collected only in down-slope and up-slope directions. Average down-slope crown radii exceeded up-slope crown radii by 20% on steep slopes, 16% on intermediate slopes, and 6% on flatter ground. Mean ratios (by plot) of down-slope crown radius to crown diameter showed a positive correlation with angle ($p = 0.01$, $r^2 = 0.3$; Fig. 3-12). These findings

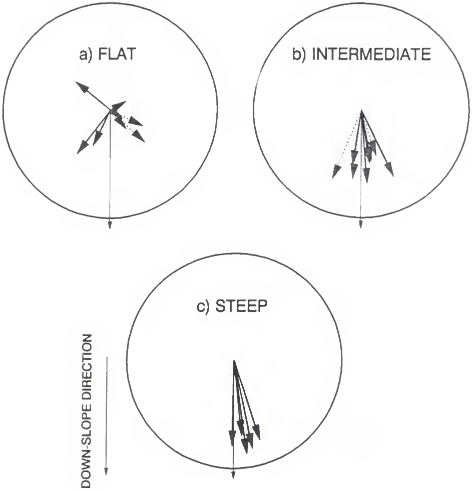


Fig. 3-11. Mean tilt direction vectors by plot (n = 60 trees) for the three slope inclinations. Mean vector directions were standardized by down-slope direction and vector magnitudes were drawn to scale setting the circle to a radius = 1. a) flat terrain (dotted arrows = flat Placudand), b) intermediate slopes (dotted arrows = east aspect), and c) steep slopes. With higher slope inclination (from a to c), both the grouping of the vectors around the down-slope direction and their respective magnitude increased.

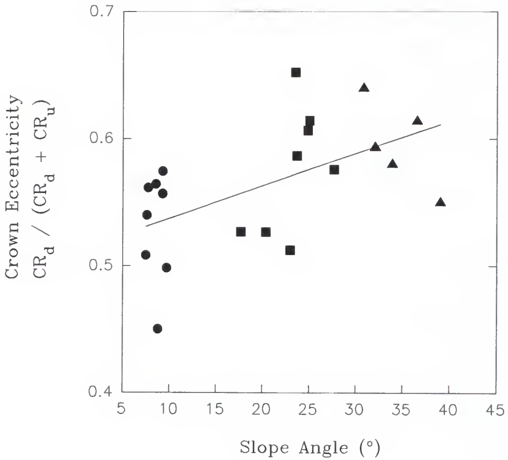


Fig. 3-12. Plot means of crown eccentricity as a function of slope ($r^2 = 0.3$, $p = 0.01$). CR_d = crown radius down-slope, CR_u = crown radius up-slope. Symbols indicate slope inclinations: ▪ flat, ● intermediate, ▲ steep.

support the hypothesis that the direction of crown eccentricity is also related to slope angle. Moreover, down-slope crown portions of canopy trees were found to overtop up-slope crown portions of adjacent down-slope trees, creating a characteristic shingling effect on slopes.

Trunk eccentricity

Mean down-slope trunk eccentricity for both flat terrain (0.99) and intermediate slope inclination (0.99) were not significantly different from 1. On steep slopes, however, eccentricity was 0.93 and stem diameters in slope direction were significantly wider than cross-slope stem diameters ($p = 0.0001$). A linear regression of plot means of trunk eccentricity by slope inclination showed a significant but weak negative correlation ($p = 0.02$). In fact, only 25% of the variation was explained by slope inclination.

Small Tree and Seedling Response to Slope Inclination (Hypothesis 3)

Small trees. Analogous to large trees, most small trees showed down-slope inclination. Leaning of small trees, including saplings, was tested for on steep slopes, ranging from 32° to 40°. Of the 240 small trees sampled on 8 transects, 96% deviated measurably from vertical. Mean tree tilt over all transects, regardless of tilt direction, was 19.4°, and mean projected tilt ($\bar{\theta}''$) on the X-Z plane (down-slope direction) was 16.7°, yielding a high ratio of mean projected tilt to mean tilt (0.85).

Mean projected tilt angles among transects ranged from 7° to 29°. This high variability is the result of the small number of trees sampled in each transect (n=30). The frequency distribution of projected tilt angle (pooled data over all transects) showed an even more pronounced skewness in the down-slope direction of the (median 11.7°), than did canopy and sub-canopy trees (Fig. 3-13).

Seedlings. Like large and small trees, seedlings tilt down-slope as well. The first-order mean of seedling tilt was 20.0° on steep slopes and 6.5° on flat ground. Projected tilt on steep slope was 16.9° (X-Z plane in down-slope direction) and -1.4° on flat ground (X-Z plane set arbitrarily in the direction of the random transects, as no down-slope direction emerged). On steep slopes, the ratio of mean projected tilt to mean tilt was 0.85, suggesting a down-slope leaning of seedlings similar to that of small trees.

On the flat area, the mean tilt direction vector had a magnitude of 0.38, reflecting a high directional dispersion of the data. Conversely, the mean tilt direction vector on steep slopes had a magnitude of 0.82 and deviated from aspect by only 7°, indicating a tight grouping of the data in the down-slope direction and a high correlation between tilt-direction and aspect. On flat ground, the frequency

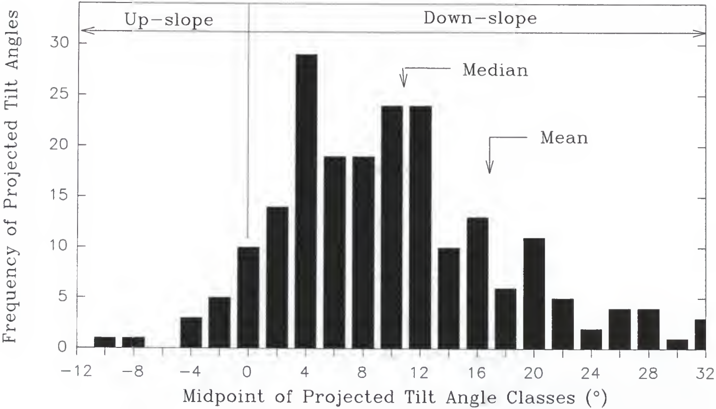


Fig. 3-13. Frequency distribution of projected tilt angles (θ'') for small trees and saplings onto the X-Z plane (down-slope) for all transects. Skewness = 2.0, mean projected tilt angle ($\bar{\theta}''$) = 16.7° and median = 10.7°.

distribution of projected tilt angles (mean -1.4°, median 0.1°) indicated normality (Shapiro-Wilk statistic, failure to reject null hypothesis, $p > 0.9$). On steep slopes, in contrast, the frequency distribution of projected tilt deviated significantly from normality ($p = 0.0001$) and was skewed in the down-slope direction (skewness 1.2, mean 16.9°, median 15.1°; Fig. 3-14). Seedlings growing on flat ground displayed moderate tilting evenly distributed around the vertical axis, whereas seedlings on steep slopes had marked down-slope tilting. The pattern is demonstrated visually using an equal-area projection of the three-dimensional unit vector on the X-Y plane (Fig. 3-15) and a three dimensional model (Fig. 3-16).

Soil Creep (Hypothesis 4)

After two years, three out of the 12 modified Young pits initially installed were excavated. Soil creep was measured as the relative down-slope displacements of the approximately 60 to 80 aluminum cylinders stacked in a straight column.

Lateral displacement (≥ 1 mm) was traceable in only 5% of the cylinders and ranged only from 1 to 2 mm. However, these few cylinders showed no up-slope or down-slope directional pattern in their displacement. It was therefore concluded that no measurable soil creep had occurred over the two year period, and excavation of the 9 additional pits

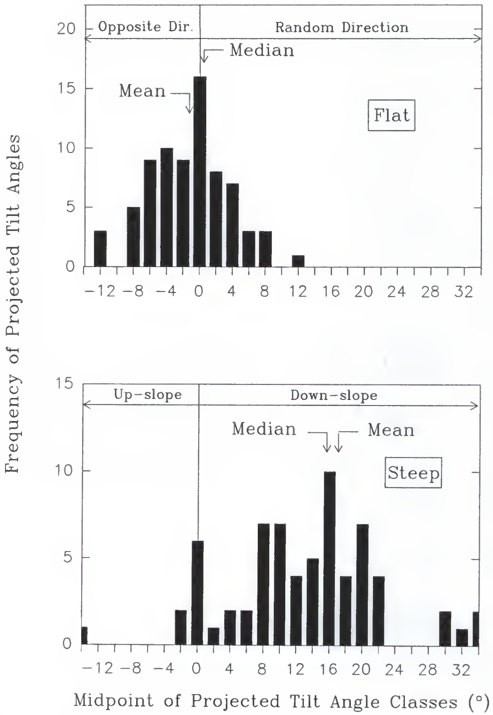
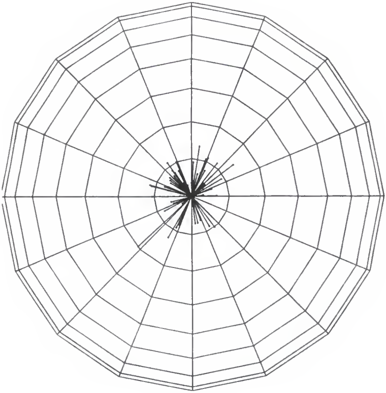


Fig. 3-14. Frequency distributions of projected tilt angles (θ'') for seedlings onto the X-Z plane (down-slope) for pooled transects over two slope categories. Flat: Projection onto plane with random direction, mean ($\bar{\theta}''$) = -1.4°, median = 0°. Steep: Projection onto X-Z plane (down-slope), mean ($\bar{\theta}''$) = 16.9°, median = 15.1°.



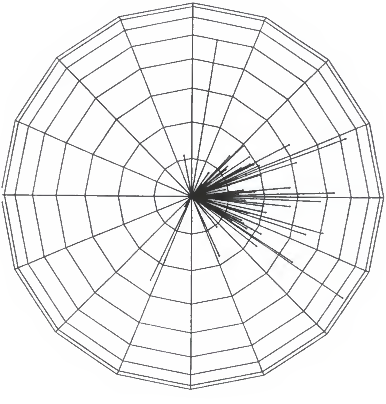


Fig. 3-15. Equal-area (Lambert) projections of seedling tilt data for flat ground (top) and for steep slope (bottom).

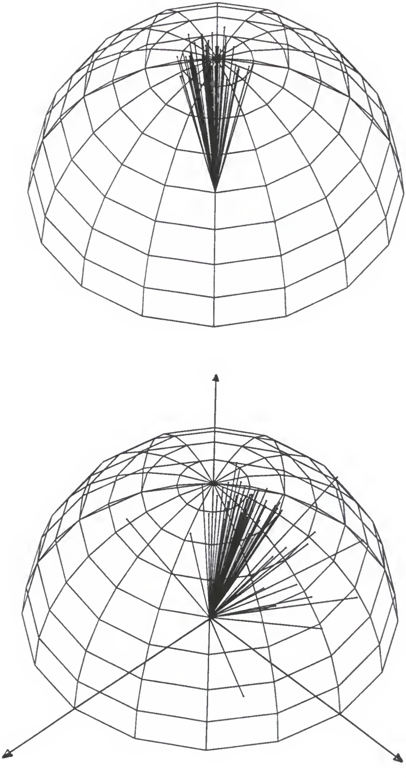


Fig. 3-16. Three dimensional model of seedling tilt data for flat ground (top) and for steep slopes (bottom).

was postponed. In general, no evidence was produced to explain tree inclination through soil creep.

Discussion

In the oak-bamboo forest of the upper Rio Macho watershed, canopy trees on steep slopes display significant down-slope stem inclination on an array of sites with disparate aspects. This pattern suggests that stem leaning is not caused by the predominantly north-east trade-winds. Moreover, down-slope tilting is highly correlated with slope angle and occurs in trees of all sizes, including saplings and seedlings. Soil creep, a mechanism often reported to cause tree leaning, was not detected by direct measurement. Moreover, bole curvature, a feature widely accepted as resulting from soil creep, was not commonly observed in these forests.

Since neither directional wind patterns nor soil creep could explain the observed tilting of trees, I hypothesize, by elimination, that asymmetric light conditions on slopes is the main force driving tree inclination. In fact, straight down-slope leaning of seedlings strongly substantiates the idea of light-induced tree leaning. Seedlings have high plasticity to reestablish orthotropic growth, and if bent by soil creep, litter flow, or other mechanical forces, are expected to display a response in form of stem curvature. However, no such feature was found, as seedlings had straight shoot axes regardless of lean.

The canopy of this montane forest had an average height of 30 to 40 m (with emergents up to 56 m) and is dominated by oak trees, whose spreading crowns occupy considerable volumes. Within crowns, leaves are mostly massed as dense subcrowns at the ends of large, gnarled limbs. This characteristic aggregated arrangement of photosynthetic tissues in space, at both stand and tree level, suggests a rather low leaf area density (Kira and Yoda 1989). These geometric peculiarities may explain the relatively low light attenuation (especially above the bamboo layer) observed in these forests, in contrast to many tropical lowland forests where direct sky-light is readily blocked by a continuous, dense canopy cover. Canopy windows (i.e., apertures in the canopy between and within crowns, through which skylight can penetrate) are a characteristic feature of these stands. I hypothesize that most of the light reaching the forest floor penetrates the canopy through such windows. Moreover, during fog-induced diffuse light conditions (common in Villa Mills) light scattering is high and even those canopy windows located at angles of low elevation could contribute substantially to the overall light influx.

On slopes I observed canopy windows to occur at lower elevation angles on the down-slope wedge of the skylight hemisphere because more self-shading vegetation impedes up-slope skylight penetration, especially at elevation angles similar to slope inclination. In a pilot study, I tested this postulate using a modified angle gauge designed for point-sample timber cruising, having an eyepiece arbitrarily calibrated to discern canopy windows with solid angles ≥ 3°. At 30 random locations on steep slopes, I conducted repeated systematic point sampling, where minimal elevation angles of the first encountered canopy windows at every 10° azimuth around the full circle were measured. A significantly lower skylight horizon occurred in the down-slope direction. From these findings, and given the suggested importance of skylight influx through canopy windows, I hypothesize that the resultant light vector on slopes is oblique and thus constitutes the main mechanism for tree inclination in the oak-bamboo forest. Further research with hemispherical photography and direct light measurements is necessary to substantiate this conclusion.

Down-slope crown eccentricity was found to be another characteristic feature of the oak-bamboo forest canopy on slopes. Data showed that down-slope crown elongation of canopy trees increases with slope angle and is independent of aspect. Tree crowns represent light gathering modules projected by trunks into a favorable light environment. On slopes this light environment is a hemisphere with a light depletion zone in the up-slope sector. Orientation of trunk axes in space, crown geometry and arrangement of crown packing all influence the efficiency of light capture. The adjacent down-slope crown may still be able to photosynthesize in the penumbra of an up-slope neighbor, yet creating a more pronounced shade for the next down-slope neighbor. I hypothesize that, to avoid light-depleted zones of closely packed crowns, trees develop crowns away from competing neighbors into the open down-slope space, producing the observed eccentric crowns and shingled canopies on slopes. Data on light and carbon budgets within canopies to substantiate this hypothesis are practically non-existent.

Both stem leaning and crown eccentricity suggest that trees on slopes are gravitationally unstable relative to trees on flat ground. To counter these disadvantageous static conditions, a substantial investment in reaction wood seems necessary, as illustrated by observed non-circular stem cross-sections. However, our full understanding of how trees on slopes are "engineered" to meet their physiological requirements is yet very incomplete. Of particular interest, for instance, is the potential support function of buttresses, because both Quercus copeyensis and Quercus costaricensis display significant leaning and crown eccentricity, but only the former has marked buttresses.

Besides static calculations on trees, long-term monitoring of tree mortality as a function of topography should help us elucidate the question of tree stability on slopes.

I suggest that geoplagiotropic trunk extension and plagiotropic crown development are advantageous in montane habitats. Similarly, but at a different scale, the down-slope arching of herbs in response to asymmetric light fields on slopes has been reported to be adaptive (Givnish 1986).

An inclined tree can theoretically support its crown at a competitive canopy height with a shorter bole than a straight tree. As an example, a down-slope leaning canopy tree of 30 m bole length (8° tilt, 35° slope) projects a crown at a height that could only be reached by a straight tree of 32.6 m. Consequently, the leaning tree would reduce the amount of supportive tissue needed, and, as hypothesized, would offset its required "investment" in tension wood. Meanwhile, with a relative height advantage of two meters, a leaning tree may reach a decisive canopy position before the potential competitor with a straight stem. The shading of the straight tree by the leaning tree may be crucial for competition, as most attenuation of light occurs at the canopy edge (Kira and Yoda 1989). In this study, no direct light measurements were conducted, and given the complexity of the processes involving light penetration and interception through tree canopies, such work is needed.

If tree leaning and crown eccentricity on slopes is advantageous for better light interception, it may in contrast reduce tree stability regardless of reaction wood. An increased probability of tree falling would lessen tree longevity and have important implications for forest dynamics on slopes. Greater treefall frequencies on slopes has been suggested by Oldeman (1978), but underlying processes and implications for forest dynamics are not well explored. I predict that the occurrence of increased treefall maintains more area in gap phase on slopes. This translates into accelerated recruitment, growth, and turnover rates and brings about more dynamic forests on slopes than on level ground. Gap and growth studies are currently being conducted to establish patterns and reveal the link of tree inclination with forest dynamics.

CHAPTER 4
EFFECTS OF SLOPE ON GROWTH, INGROWTH, AND MORTALITY

Introduction

Tree population dynamics in natural forests are driven by geological, geomorphological, climatic, and pedological factors, but most of all by natural disturbances (Pickett and White 1985). Disturbances maintain landscape mosaics and forest structure in dynamic flux and periodically modify abiotic and biotic conditions influencing plant development. Composition is also important, as the above factors can only operate on the species that are present, and highly variable responses can result from different species' life histories (Whitmore 1990). In combination, these factors determine regeneration, growth, and mortality, and control forest composition, structure, and turnover in both time and space.

Landscapes prone to large-scale disturbances (e.g., hurricanes, fires, landslides, insect outbreaks) can be described as coarse-grained, heterogenous mosaics. They tend to have large patches of relatively even-aged stands of species adapted to exploit highly disturbed, open habitats (Runkle 1985, Denslow 1985). Landscapes affected by small-scale disturbances (e.g., wind gusts, lightning, soil creep, non-epidemic pathogens) exhibit fine-grained, relatively homogeneous mosaic patterns with small treefall patches within a matrix of mature forest (Denslow 1985). In the latter case, background mortality is continually balanced by new recruits at the local level of small-sized treefall or multiple treefall gaps. Such a fine-grained forest may attain steady-state (Swaine et al. 1987) at a relatively small scale and can be described by simple mosaic-cycle forest models (Wissel 1991).

Topography can play an important role in shaping tree population dynamics and forest community structure (Whittaker 1975). In the tropics, the little research on topographic effects on vegetation has focused on unstable slopes subjected to rapid mass movement that brings about patchy, coarse-grained landscapes (Garwood et al. 1979, Guariguata 1990). The role of topography in stable landscapes, where slope may create specific environmental conditions that induce differential tree population dynamics in space, has not been adequately explored (but see Hubbell et al. 1991) and is the subject of this study.

In the oak-bamboo forest of the upper Rio Macho watershed in Costa Rica, where this study was conducted, there are no apparent signs of recent intense, large-scale disturbances or forest die-back. The canopy is closed and continuous, and the forest is surprisingly homogeneous in structure and composition. Despite rugged terrain, the forest is visibly disrupted only in the vicinity of steep gullies, where bank erosion causes more disturbances. In the oak-bamboo forest of the upper Rio Macho watershed, mortality occurs mainly at the individual tree level, and dead trees are predominantly replaced by other oaks.

As a result of the low intensity disturbance regime and apparent homogeneity of the landscape (sensu Forman and Gordon 1986), it would seem sensible to conclude that this old-growth forest has reached a shifting-mosaic steady-state at the landscape level (sensu Bormann and Likens 1979). This conclusion, however, would be inaccurate if tree populations are, in fact, differentially responding to effects of the sloping topography. In such a landscape, it may be critical to incorporate spatial stratification based on topography into models of tree population dynamics.

My hypothesis was that slope induces differential local tree growth, mortality, and turnover times. This overall hypothesis was broken down into three testable predictions: 1) individual tree and stand growth increase with slope, 2) the rate of ingrowth into the smallest defined diameter class increases with slope, and 3) mortality rates increase with slope. Support for these three hypotheses would be taken as corroboration of the overall hypothesis that forests on slopes are more dynamic than forests on level terrain.

Study Site and Methods

Study Site

The field research was conducted in the oak-bamboo forest described in Chapter 2. In 1987/88, 21 permanent 1-ha plots were established within the study area (Fig. 4-1). The plots were established following a design that included three levels of inclination: flat (0° to 10°), intermediate (15° to 25°) and steep (30° to 40°). The three treatments were replicated five times each. Altitude (2750 m ± 100 m), aspect (west facing) and soil type (Hapludand) were kept constant. In addition, the flat treatment was repeated three times on a different soil type (Placudands), and the intermediate treatment on a contrasting aspect (east-facing), to test for potential secondary effects of these factors. These two secondary treatments are hereafter referred to as "Placudand" and "east aspect".

The Placudand treatment was included to investigate a possible effect of this soil contrast on the phytosociological associations within the level portion of the study area (Blaser 1987, Blaser and Camacho 1991). The east aspect was included to assess effects due to aspect-related differences in solar irradiation. (Because of the low latitude of the study site, the solar path has little seasonal north-south deviation, and as a result of regular

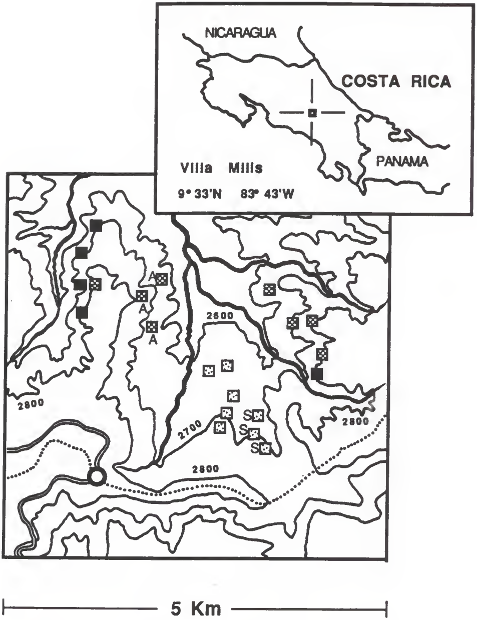


Fig. 4-1. Study area and plot location: (○) The hamlet of Villa Mills, Upper Rio Macho Watershed, Cordillera de Talamanca, Costa Rica. (……) The Continental Divide. Squares indicate 1-ha study plots with slope inclinations (i.e., treatments): (⊡) = flat (0° to 10°), (▨) = intermediate (15 to 25°), and (■) = steep (30° to 40°). Additional plots for testing secondary effects of soil and aspect are indicated with (S) and (A).

afternoon cloudiness, east-facing slopes receive far more insolation than west-facing ones.)

Plot Establishment

Plots were established within an altitudinal belt ranging from 2800 to 3000 m following a stratified random process. On a 1:50000 map (ING-CR 1955), the study area was broken up into units incorporating the three slope inclinations, the two aspects, and the two soil types. A strip of human-disturbed forest near the continental divide and gullies with steep, eroded banks were excluded. Plot corners were then randomly selected on the map and their location in the field identified with compass and hip chain (Fig. 4-1).

To avoid extreme deviations from the prescribed slope classes (e.g., gullies not shown on the map), plots were assembled from subplots of 20 m by 25 m. Subplots were added one at a time into available area from the plot corner in the down-slope direction. Subplot arrangement followed a random algorithm with restrictions that would produce plots with highest possible area to edge ratio. Nevertheless, many non-square plots resulted.

Plot Inventories

In 1987/88, all trees ≥ 10 cm diameter at breast height (dbh; measured at 1.3 m above the ground or above buttresses) were identified to species and numbered with aluminum tags attached 1.5 m above the ground. Dbh was measured to the nearest millimeter with steel tapes. Trees with buttresses rising above breast height were measured at least 20 cm above the end of the highest buttress at standard heights of either 2 m, 2.5 m, 3 m, etc., up to 6 m (Synott 1979). All trees were permanently marked at the measurement point by painting a ring around the trunk.

In 1989/90, a second complete inventory of the plots was conducted and diameters of all initially tagged, live trees (henceforth referred to as residual trees) were remeasured. Recruits, including ingrowth into the 10 cm dbh class and trees that had been overlooked during the first inventory, were identified, tagged, painted, and measured. Dead trees were counted and their condition (uprooted, snapped, or standing) was recorded. Residual trees whose second diameter measurement yielded questionable diameter change were remeasured and potential reasons were evaluated. Aberrant values resulting from obvious stem abnormalities (e.g., bark stripped off, cambial protuberance) were reported as such but coded as invalid values during subsequent growth analysis.

For calculations, only the values of annual diameter increment ranging from -0.8 cm to 1.5 cm were retained, based on an analysis of the growth data. Application of this conservative filter resulted in the deletion of only 15 apparently aberrant outliers (0.17% of the sample population).

Based on maximum annual growth, trees that grew into the 10 cm class over the course of the study had to be differentiated from those whose large diameter suggested that they were overlooked during the 1987/88 inventory. The discriminating filter used above (i.e., maximum annual diameter growth of 1.5 cm or maximum possible dbh of ingrown tree after 1 year of 11.5 cm) was liberal in this context, as it tended to overestimate the amount of ingrown trees. Moreover, trees were more likely to have been overlooked on steep slopes due to reduced visibility and increased fatigue of researchers. This may have created a bias in favor of hypothesis H_2 (increased ingrowth on slopes) because inflated ingrowth values on slopes could mistakenly be attributed to a treatment effect. Therefore, separation of ingrowth and residual trees was based upon a more conservative cutoff point set at 10.5 cm maximum dbh of ingrown trees after 1 year.

For hypothesis testing, "growth" was expressed as either diameter increment, basal area increment, or relative growth rate of either of those two variables over the measurement interval recorded for each tree. Since diameter increment does not take plant performance in relation to size into account, it was used to assess treatment effects within diameter classes only. In contrast, basal area increment in a sense weights growth performance of large trees more heavily than small trees. In this study, basal area increments were used to compare responses to slope only after an initial multivariate analysis of variance determined that differences in diameter class frequency distributions among the three slope classes were insignificant. Relative growth rate (RGR) expresses growth performance of a tree by taking into account its size at the start of the interval. It is defined as the slope of a curve relating the logarithm of diameter or basal area to time (Hunt 1978). RGR is a good estimator for comparing treatment differences within polyspecific, uneven-aged communities, which is how it was used.

For estimation of basal area and basal area increment on steep slopes, non-circularity of tree cross-sections was also taken into account (Husch et al. 1982, Biging and Wensel 1988). In a concurrent study on tree leaning and crown eccentricity (Chapter 3), I found significantly greater down-slope stem eccentricity for individual trees (measured as the ratio of the smallest dbh to the largest dbh) on steeper slopes (average eccentricity on slopes > 30° was 0.93). Girth measurements conducted on out-of-round trees overestimate true basal areas and would constitute a bias in favor of the growth-related hypotheses. Therefore, prior to statistical analysis, basal area values on steep slopes were corrected by taking the above factor into consideration.

Mortality rate was calculated as the progressive loss of trees from the initial plot populations using a model based on a logarithmic decline of tree numbers with time and expressed as the following equation (Swaine et al. 1987):

$$m = 100\ (\ln n_0 - \ln n_1)\ \frac{365}{t}$$

where n_0 is the number of trees alive at the first census, n_1 is the number of trees alive at the second census, and t is the census interval in days. The same model was used to calculate stand half-life, defined as the number of years required for a population to fall to 50% of its initial level.

Given the large total number of trees measured, the 1987/88 inventory was conducted in two steps, starting with the tallying of large trees (≥ 20 cm dbh) and ending with small trees (10 to 20 cm dbh). The mean amount of time elapsed between first and second inventories of larger and smaller trees was 700 and 500 days, respectively. Taking this into account, the mortality rate was calculated separately for these two sub-populations.

Results

Species Composition

A total of 8793 and 8928 live trees ≥ 10 cm dbh were measured in the 1987/88 and 1989/90 inventories, respectively. The difference was a result of the loss of 94 trees through mortality, ingrowth of 233 new trees into the 10 cm dbh class, and rejection of four small trees whose second measurement was < 10 cm dbh as a result of shrinkage. The total number of species (Table 1) did not change over time, and included 46 species in 39 genera and 32 families. For the first inventory, mean values over all plots were 26 species ha^{-1}, 419 stems ≥ 10 cm dbh ha^{-1}, and a basal area of 47 m^2 ha^{-1}. Species richness, stem density, and basal area varied among replicates and treatments (Table 1).

The two oaks comprised close to 90% of the total basal area, although their proportions varied considerably among plots. Quercus copeyensis was the dominant tree, accounting for 75% of the basal area and 42 % of the stems. Quercus costaricencis, was second in dominance, accounting for 13% of the basal area and 7% of the stems (Fig. 4-2).

Species richness increased with steepness of slope ($r^2 = 0.41$, $p = 0.01$). Stem densities, however, did not differ significantly with slope ($r^2 = 0.06$, $p = 0.27$), and basal area was significantly higher on flat ground ($r^2 = 0.32$,

Table 4-1. Characteristics of the 21 permanent plots of the tropical montane oak-bamboo forest at Villa Mills, Costa Rica. Data refer to stems $\geq$ 10 dbh. TRT = treatment, REP = replicate, $\bar{x}$ = mean, QCP = Quercus copeyensis, QCR = Q. costaricensis.

			INVENTORY 1987/1988							INVENTORY 1989/1990						
TRT	REP	SLOPE ANGLE	NO. SPP	NO. STEMS	% STEMS QCP	% STEMS QCR	BASAL AREA (m2)	% BASAL AREA QCP	% BASAL AREA QCR	NO. SPP	NO. STEMS	% STEMS QCP	% STEMS QCR	8ASAL AREA (m2)	% 8ASAL AREA QCP	% 8ASAL AREA QCR
FLAT	1	9.5	23	355	65	1	64.9	89.2	2	24	359	64.6	1.4	64.9	89.0	1.9
FLAT	2	8.5	19	348	70	0	50.8	92.7	0	19	352	69.9	0.0	51.2	92.6	0.0
FLAT	3	9.5	16	427	66	0	56.4	85.9	0	16	425	66.8	0.0	56.3	86.3	0.0
FLAT	4	9.0	20	369	59	1	42.6	86.6	1	20	371	58.8	0.5	43.0	86.7	0.9
FLAT	5	9.5	15	506	59	1	51.1	85.2	2	15	505	58.8	1.4	49.9	84.6	2.6
$\bar{x}$	1-5	9.2	19	401	64	1	53.2	87.9	1	19	402	63.8	0.7	53.1	87.9	1.1
FLAT	6	7.5	22	545	37	16	51.5	54.9	28	22	556	37.1	15.5	51.4	55.5	27.1
FLAT	7	7.5	19	466	34	19	49.0	40.3	46	19	472	33.3	18.6	48.6	39.2	46.4
FLAT	8	7.5	21	464	38	9	52.1	66.2	16	21	475	38.1	8.4	51.3	67.8	13.7
$\bar{x}$	6-8	7.5	21	492	36	14	50.8	53.8	30	21	501	36.1	14.2	50.4	54.2	29.1
$\bar{x}$	1-8	8.6	19	435	54	6	52.3	75.1	12	20	439	53.4	5.7	52.1	75.2	11.6
INTER	9	17.5	17	397	46	3	43.8	71.6	7	18	400	46.0	2.5	44.3	71.4	7.4
INTER	10	20.5	23	350	46	0	50.1	82.1	0	26	360	45.3	1.9	50.8	81.8	6.7
INTER	11	23.0	22	475	59	0	46.1	83.8	0	23	482	58.3	0.2	46.5	83.6	0.4
INTER	12	23.5	17	325	0	33	33.2	0.0	68	17	335	0.0	32.8	33.5	0.0	67.8
INTER	13	25.0	21	365	46	5	52.1	72.4	11	21	372	45.7	5.1	52.6	72.3	10.9
$\bar{x}$	9-13	21.9	20	382	39	8	45.1	62.0	17	21	390	39.1	8.5	45.5	61.8	18.6
INTER	14	23.5	19	488	58	1	56.9	82.1	3	19	503	57.5	1.2	57.6	81.9	2.9
INTER	15	25.0	18	537	24	19	46.0	39.7	36	18	548	23.7	18.8	45.5	40.6	35.0
INTER	16	27.5	18	478	26	13	47.1	50.2	27	21	488	25.6	12.7	47.4	50.6	26.9
$\bar{x}$	14-16	25.3	18	501	36	11	50.0	57.3	22	19	513	35.6	10.9	50.2	57.7	21.6
$\bar{x}$	9-16	23.2	19	427	38	9	46.9	60.2	19	20	436	37.8	9.4	47.3	60.3	19.8
STEEP	17	31.0	28	401	41	3	41.4	68.4	10	28	407	41.5	3.2	41.3	68.1	10.4
STEEP	18	32.0	26	381	2	17	27.2	3.0	46	27	397	1.5	18.1	27.3	3.1	44.2
STEEP	19	34.0	23	327	54	0	46.5	85.7	0	23	328	52.4	0.0	43.1	84.3	0.0
STEEP	20	36.5	30	357	8	6	30.5	26.2	11	30	363	8.0	6.1	30.3	26.5	11.0
STEEP	21	39.0	34	432	39	0	44.3	70.9	0	34	433	38.8	0.0	44.8	71.1	0.0
$\bar{x}$	17-21	34.5	28	380	29	5	38.0	50.8	13	28	386	28.5	5.5	37.4	50.6	13.1
$\bar{x}$	1-21	20.3	21	419	42	7	46.8	63.7	15	22	425	41.5	7.1	46.7	63.7	15.1

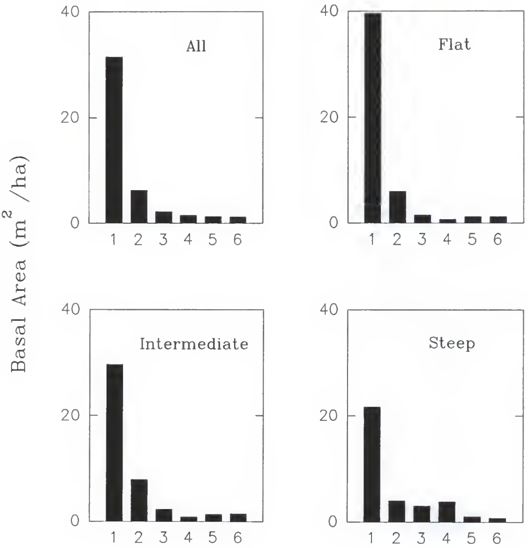


Fig. 4-2. Basal area for whole the forest (all) and for each slope category (flat, intermediate, steep) including the 5 most important species and the pooled residual species: (1) Quercus copeyensis, (2) Quercus costaricensis, (3) Weinmannia pinnata, (4) Residual species, (5) Styrax argenteus, and (6) Phoebe pittieri.

p = 0.01). Despite these differences, diameter class distributions of trees ≥ 10 cm did not differ significantly among treatments (MANOVA, Wilks' Lambda, p = 0.2). Diameter class frequencies exhibited negative exponential distribution (Fig. 4-3), well fitted by a linear regression of the log-transformed tree frequencies against the midpoint values of diameter classes ($r^2 = 0.92$, p = 0.0001). This indicated a balanced ratio of small trees to large trees, characteristic of many undisturbed, mixed even-aged forests.

Growth

Mean annual diameter increment of the 14 most abundant tree species (species occurring at frequencies ≥ 1% of the pooled data) ranged from 0.1 to 0.4 cm and differed markedly among species and treatments. For most species, mean annual growth tended to increase with slope (Fig. 4-4).

The mean annual RGR of diameter of the pooled species (all diameter classes included) showed a significant increase with slope ($r^2 = 0.63$, p = 0.0001; Fig. 4-5, top). Moreover, Q. copeyensis, a species sufficiently well represented to yield reliable plot means in most replications, was analyzed alone to control for a possible species effect, and showed the same significant pattern of increased growth on slopes ($r^2 = 0.60$, p = 0.0001; Fig. 4-5, bottom).

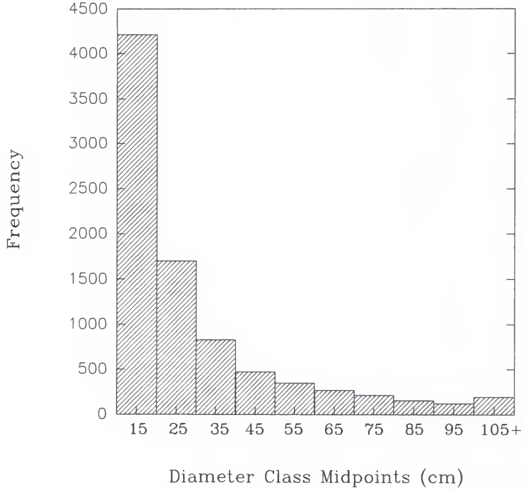


Fig. 4-3. Overall diameter class distribution for trees ≥ 10 cm dbh from the 1987/88 inventory (21 1-ha plots, n = 8669 trees).

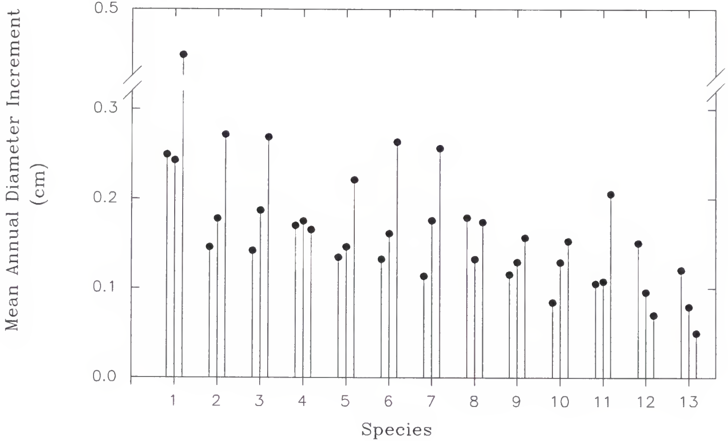


Fig. 4-4. Trunk growth as a function of slope for the 13 most abundant species (stem density ≥ 1%). Bars grouped by treatment from left to right: "flat", "intermediate", and "steep".

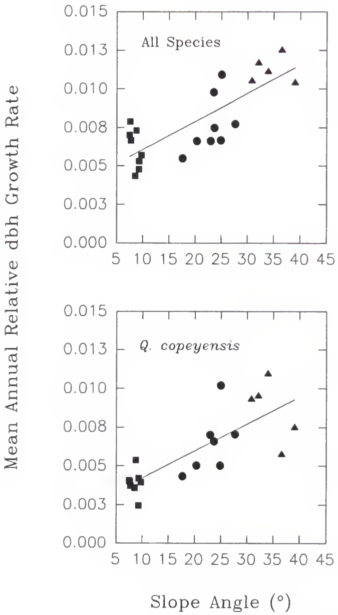


Fig. 4-5. Plot means of relative annual stem diameter increment by slope. Top: Pooled species ($r^2 = 0.63$, $p = 0.0001$). Bottom: Quercus copeyensis ($r^2 = 0.60$, $p = 0.0001$). Symbols indicate slope inclinations: ■ flat, ● intermediate, ▲ steep.

To determine whether tree size affected diameter growth, mean annual diameter increments of pooled species and _Quercus_ _copeyensis_ alone were further analyzed by diameter class. For both samples, mean annual diameter increment was significantly higher on slopes in all dbh classes up to 55 cm (ANOVA, all species, $p = 0.005$, Fig 4-6, top; _Q_. _copeyensis_, $p = 0.005$, Fig. 4-6, bottom). The pattern of increased growth on slopes was not observed in the very large trees (> 70 cm dbh). This is attributed to the small sample size and the difficulty of accurately measuring large, buttressed trees. In all treatments, annual diameter growth increased with ascending diameter class up to the 55 cm, beyond which no precise inferences could be drawn due to the high variance.

These findings suggest that trees with intermediate diameters ranging from 40 to 70 cm play an important role in the overall growth performance of these old-growth forests. Therefore, a growth comparison of basal area increment by treatment was imperative, even though diameter class distributions did not differ significantly among the treatments. Mean basal area increment of all residual trees, as well as _Q_. _copeyensis_ separately, also showed a highly significant increase with slope (regression of plot averages, all species, $r^2 = 0.87$, $p = 0.003$, Fig. 4-7, top; _Q_. _copeyensis_ separately, $r^2 = 0.60$, $p = 0.0001$, Fig. 4-7 bottom).

Fig. 4-6. Mean annual diameter increment for slope treatments by dbh classes. Top: All species. Bottom *Quercus copeyensis*. Differences among treatments (ANOVA by diameter classes) were significant for all diameter classes up to 55 cm. Symbols indicate slope inclinations: ▪ flat, ● intermediate, ▲ steep.

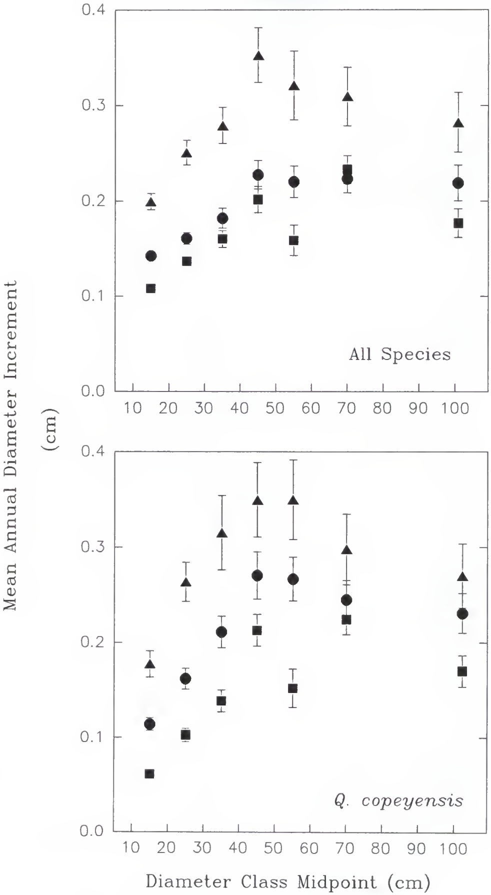
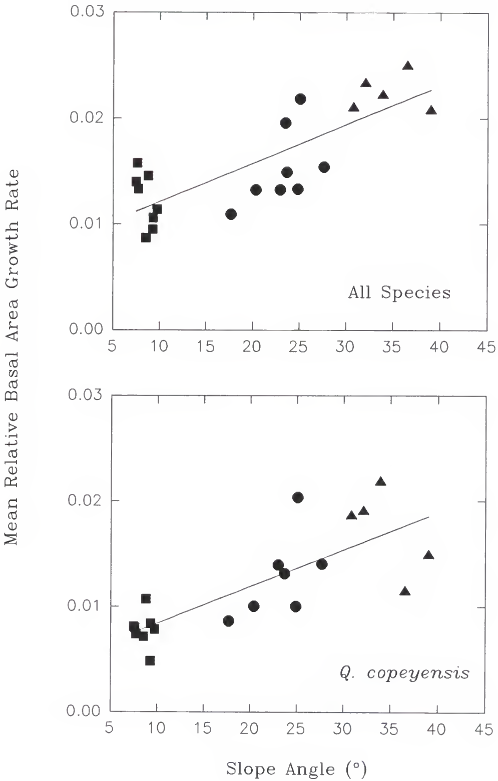

Mean Annual Diameter Increment
(cm)
0.0
0.1
0.2
0.3
0.4
10
20
30
40
50
60
70
80
90
100
All Species
Q. copeyensis
Diameter Class Midpoint (cm)

Fig. 4-7. Linear regression of plot means of annual relative growth rate plotted as a function of slope angle. A) Pooled species ($r^2 = 0.63$, $p = 0.001$). B) *Quercus copeyensis* ($r^2 = 0.60$, $p = 0.0001$). Symbols indicate slope inclinations: ■ flat, ● intermediate, ▲ steep.


Mean Relative Basal Area Growth Rate
0.03
0.02
0.01
0.00
5
10
15
20
25
30
35
40
45
All Species
Q. copeyensis
Slope Angle (°)

Despite significantly lower basal area on slopes, the total basal area increment of residual trees of all species pooled and of Q. copeyensis alone was higher on slopes (regression of plot averages, all species, $r^2 = 0.78$, $p = 0.05$; Q. copeyensis, $r^2 = 0.26$, $p = 0.02$; Fig. 4-8), suggesting higher absolute forest productivity on the steeper terrain.

Recruitment

The total number of new trees tallied in the second inventory amounted to 357 trees ≥ 10 cm dbh. Of these, 154 were true ingrowth trees into the 10 cm diameter class and 203 were trees missed in the first inventory (based on the discrimination filter of ingrowth ≤ 10.5 cm dbh). The mean number of ingrowth trees differed significantly between the two soil types (t-test, $p = 0.008$) and aspects (t-test, $p = 0.003$), indicating that a soil or aspect effect on ingrowth could not be ruled out. Consequently, for the analysis of treatment effects on ingrowth, these secondary treatments were not pooled with the three basic slope categories.

Among the overlooked trees, more trees were missed on steep slopes (least squares means, $p = 0.03$). This may have produced an overestimation of the number of ingrown trees on slopes, introducing a bias in favor of the hypothesis of increased ingrowth on slope. The use of the very conservative filter separating ingrown trees from overlooked

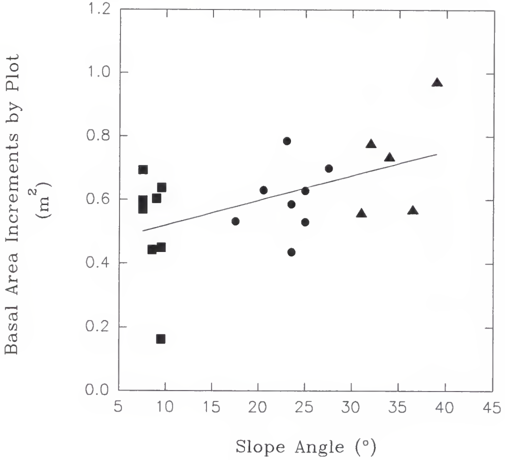


Fig. 4-8. Basal area increments by plot as a function of slope inclination ($r^2 = 0.26$, $p = 0.02$). Symbols indicate slope inclinations: ▪ flat, • intermediate, ▲ steep.

trees, set at the cutoff limit for ingrowth at 10.5 cm dbh, is considered to have reduced the bias as much as possible. Linear regression of plot means of ingrown trees by slope angle showed a significant positive effect of slope ($r^2 = 0.53$, $p = 0.001$; Fig. 4-9).

Mortality

Between the 1987/88 and 1989/90 inventories (mean period of monitoring 606 days), mortality amounted to 94 trees out of the 8669 trees alive during the first census (the 124 overlooked trees were not included). Taking the different inventory intervals of large trees (≥ 20 cm dbh) and small trees (10 to 20 cm dbh) into account, this total number was comprised of 56 dead from among the large trees (4321 trees initially alive, $t = 704$ days) and 38 dead from among the small trees (4348 initially alive, $t = 504$ days).

Large trees were no more likely to die than small trees: annual mortality rates of large and small trees were estimated at 0.67 and 0.64, respectively. Mortality frequency distributions for each diameter class were similar to live tree frequency distributions, further illustrating the lack of a relationship between mortality and tree size (Fig. 4-10). Consequently, for trees ≥ 10 cm, the pooled data ($n_t = 8669$, $n_m = 94$) were adequate for calculation of overall mortality rate ($m_t = 0.655$) and population half-life ($t_{0.5} = 107$ years).

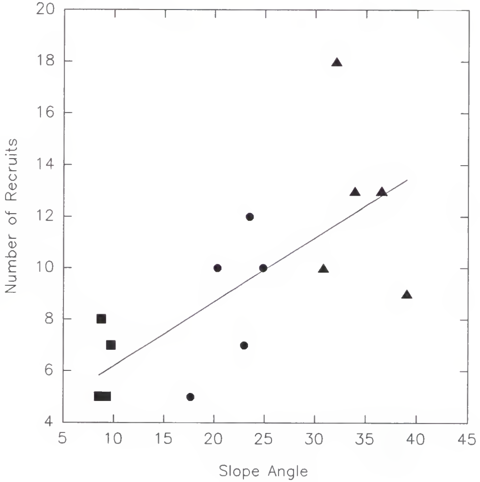


Fig. 4-9. Linear regression of the number of ingrown trees into the 10 cm diameter class as a function of slope inclination over the period between the 1987/88 and 1989/90 inventories ($r^2 = 0.53$, $p = 0.002$). Symbols indicate slope inclinations: ■ flat, ● intermediate, ▲ steep.

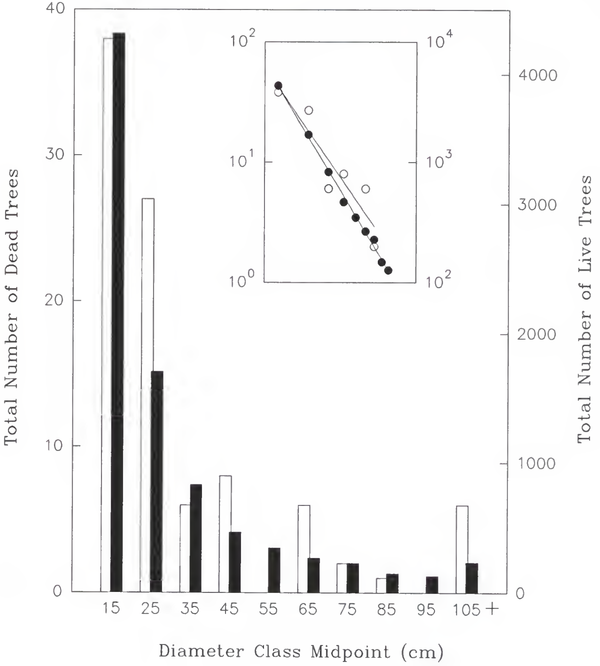


Fig. 4-10. Mortality frequency and overall tree frequency (21 ha totals) by diameter class. Inset: Same data plotted on logarithmic scale. White = dead trees, black = live trees.

The hypothesized positive relationship between plot level mortality rate and slope inclination was not significant ($r^2 = 0.02$, $p = 0.59$; Fig. 4-11). Nevertheless, when mortality rates were calculated from pooled mortality data by slope categories, steep slope exhibited the highest value for ($m_{flat} = 0.72$, $m_{inter} = 0.47$, and $m_{steep} = 0.89$). This suggests that a trend of higher mortality on slopes may be emerging, but that monitoring mortality over a longer time period is required before the mortality hypothesis can be tested with confidence.

Of the trees that died, 29% snapped, 37% were uprooted, and 32% died standing, suggesting no prevalent mode of death (Fig. 4-12). Association between slope inclination and death mode was only moderately significant (Fisher's Exact Test $p = 0.085$). Assuming the association is significant, a subsequent Maximum Likelihood Analysis showed a significant contrast between standing dead trees on flat and steep terrain ($p = 0.02$). Given the small sample size, however, the conclusion that the "standing dead" condition is more likely to occur on flat ground than on steep slopes is doubtful. Analogous analysis for large trees (≥ 20 cm dbh) and small trees (10 to 20 cm dbh) could not be conducted because the number of dead trees in these separate classes was too low. Furthermore, mortality did not appear to affect one species more than others, and no pattern with

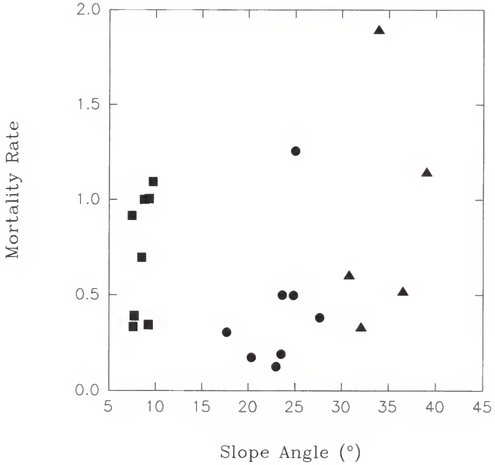


Fig. 4-11. Plot-level mortality rate by slope angle (r^2 = 0.02, p = 0.59). Symbols indicate slope inclinations: ▪ flat, ● intermediate, ▲ steep.

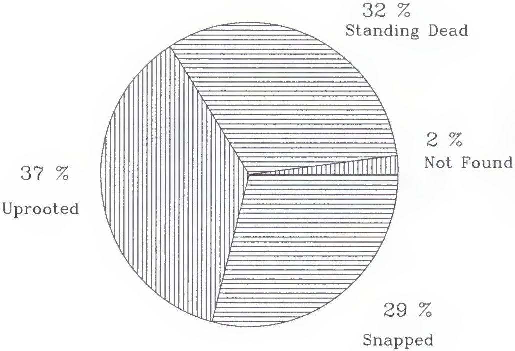


Fig. 4-12. Modes of death of all dead trees (21 plot totals, n = 94 trees). Trees "not found" were apparently shattered and buried by large fallen trees.

topography could be identified. Among the 94 dead trees, 12 species were represented.

Initial overall mean basal area of 46.84 m^2 ha^{-1} ($\geq$ 10 cm dbh) and the final mean basal area of 46.86 m^2 ha^{-1} (live trees $\geq$ 10 cm dbh, ingrowth included) were almost identical. Basal area showed considerable variation among plots, but overall basal area increment including ingrowth was closely offset by mortality.

Discussion

Overall, slope angle explained a high degree of the variability of both tree growth and recruitment. The RGR of all trees (pooled by species and diameter) was significantly higher on slopes. The same pattern was found to be highly significant for the most dominant single species, Quercus copeyensis. In addition, significantly greater annual diameter growth on slopes was found up to the 55 cm diameter class for all species pooled as well as for Q. copeyensis alone. Furthermore, RGR of basal area of residual trees followed the same patterns, suggesting that biomass accumulation of these trees is substantially higher on slopes. The ingrowth data supported these findings, as the number of ingrowth trees was significantly higher on slopes. In contrast, no significant relationship between mortality rate and slope was established. This result, however, came as no surprise, as the period of monitoring was too short to accommodate what are expected to be substantial spatial and temporal fluctuations in mortality, (Sollins 1982, Swaine et al. 1987). In fact, a few large fallen trees caused the death of many other trees, making the mortality data among plots quite variable. A more reliable test of the mortality hypothesis should therefore be based on mortality data collected over a much more extended period.

In general, the high levels of significance by which both the growth and ingrowth hypotheses were supported are strong evidence in favor of the overall hypothesis that local tree populations are more dynamic on slopes than on flat areas. Moreover, failure to reject the null hypothesis of equal mortality over all treatments, based on such a brief study, does not outweigh the highly significant results pertaining to differential growth and ingrowth. I conclude that tree population dynamics of these forests was positively correlated, and turn-over time negatively correlated, with slope.

The general pattern that slope induces faster growth, increased ingrowth, and shorter turn-over times has implications for the design of mosaic-cycle models of montane forests. Simple mosaic-cycle models should not be mechanically applied over entire mountainous landscapes but should incorporate the variability resulting from topography into their design. In fact, models of forested landscapes with rugged terrain may require previous topographic spatial stratification, because slope may constitute a key factor affecting population dynamics.

The results of this study are statistically representative for the study area. However, an unavoidable treatment segregation, characteristic of most mensurative studies (Hurlbert 1984), resulted from the spatial arrangement of topography over the study area. Plots situated in the south-east corner of the study area (Fig. 4-1) differed in species composition from other plots, particularly in having a higher proportion of *Quercus costaricensis* relative to *Q. copeyensis*. In a previous study of the forest in the flat portion of the study area, Blaser (1987) and Blaser and Camacho (1991) explained the higher concentration of *Q. costaricensis* there as a soil-related phytosociological association. Based on my sampling, however, I found this correlation to be weak, as steep slopes were predominantly associated with Hapludands (rather than Placudands), but still had high *Q. costaricensis* densities. Without denying the possibility of a plant-soil association on the flat area, it seems that large *Q. costaricensis* stands, confined to the more elevated foot slopes of the "Cerros Cuericí" (in which *Q. copeyensis* is not represented), led to an increased abundance of *Q. costaricensis* in this portion of the study area. Overall, however, treatment segregation apparently introduced no serious bias, as stem density, basal area, and diameter class frequencies displayed low variability among replications. Furthermore, the south-east corner of the study area contains plots of all slope classes, distributing any potential location bias over all treatments.

In general, this study demonstrated the pattern, rather than the process, of increased local turn-over rates of the oak-bamboo forest on slopes. The underlying processes are undoubtedly multifaceted, and will require further investigation to be fully elucidated. At this stage, however, several mechanistic hypotheses can be formulated.

Two above-ground processes are likely to be responsible for observed growth patterns. First, certain architectural responses of trees on slopes can increase light capture and accelerate tree growth. In particular, ambient light capture on slopes is assumed to be optimized by down-slope tree leaning and crown eccentricity (Chapter 3). In closed forest on slopes, crowns of canopy trees are staggered and receive full overhead as well as lateral light in their down-slope portions. On flat ground, in contrast, most canopy trees have only the top of their crown exposed to full light and experience substantial lateral shading by neighbors. Decreased crown competition on slopes through better spatial arrangements may produce increased growth. The importance of crown position to individual tree growth is well documented in the tropical silvicultural literature (e.g., Dawkins cited in Synott 1979) and is believed, after crown size and health, to play an important role in growth performance.

A second explanation takes into account the preliminary results of a gap mapping conducted on the same plots, which suggest that, relative to flat areas, a higher percentage of forest areas on slopes is in gap phase. This brings about an increased proportion of gap and edge conditions, more favorable for rapid tree growth, on slopes. If this is true, isolated gap survivors and edge trees would be responsible for the observed accelerated tree growth on slopes. In the current study, growth was analyzed without taking into account tree position with respect to gaps, so that further research is needed to test this hypothesis. An ongoing activity is the scoring of trees with respect to light availability through the overlaying of tree distribution maps on gap maps; this should provide the necessary database to test the correlation between canopy openings and tree growth on slopes.

In terms of below-ground factors, two further hypotheses emerge. First, I have observed that on slopes, substantial amounts of humus and organic debris are transported by rainwater runoff and deposited on the uphill side of trees, often caught in pockets between buttresses. Given the size and longevity of the trees involved, these "nutrient traps" seem to be substantial, as they produce a characteristic terracing of slopes. Fine roots are observed to be extremely dense in these organic matter traps, providing trees on slopes with a potential nutritional advantage.

Second, assuming similar horizontal spacing of trees on both sloped and flat ground, the available soil space on slopes is increased by the reciprocal value of the cosine of the slope inclination (e.g., the orthogonal projection of a given horizontal area onto a steep plane of 35° inclination is 22% larger). In montane forests, where fine roots are confined to the upper soil level (Jordan 1985, Whitmore 1990), an extension of available space could significantly reduce root competition and give trees on slopes a competitive advantage. In green house experiments, below-ground soil space availability has been linked with plant performance (McConnaughay and Bazzaz 1991).

These hypotheses are not mutually exclusive and interactions among the processes are likely to occur. Further studies will be needed to disentangle these relationships.

CHAPTER 5
SYNTHESIS

The primary objective of this study was to test the effect of slope on tree dynamics of oak-bamboo forests of the Upper Río Macho watershed. To test this overall hypothesis, a logical tree, sensu Platt (1964), was constructed and broken down into three sets of hypotheses, including the effects of slope on tree geometry (H_1, H_2, H_3), gap-phase processes (H_4, H_5), and tree population dynamics (H_6, H_7). The findings of the tests of these hypotheses are summarized as follows.

Tree Geometry

H_1: Down-slope tree leaning is positively correlated with slope angle and is independent of aspect. This pattern holds true over all tree sizes, including seedlings, and its underlying process is hypothesized to be a geoplagiotropic growth response to the asymmetric light environment on slopes.

H_2: Mature trees display down-slope eccentricity of crowns, hypothesized to result from plagiotropic crown development away from competing, overtopping neighbors.

H_3: Trunk cross-sections on steep slopes are non-circular, with largest diameter in the down-slope direction. It is believed that trees on slope had developed reaction wood to counterbalance the moment resulting from tree leaning and crown eccentricity.

Tree Population Dynamics

H_6: Relative diameter-growth rates of forests are positively correlated with slope and are roughly double those of forests on flat ground.

H_7: The number of trees growing into the 10 cm dbh class is positively correlated with slope inclination. Together, H_6 and H_7 strongly suggest that stand turnover is higher on slopes.

H_8: Mortality rates did not show significant statistical differences among slope inclinations. Failure to reject the null hypothesis of equal mortality rate was mostly attributed to the brief duration of the study (2 years) and the resulting marginally small sample size (n = 94 dead trees). Furthermore, variance of mortality per plot was high, as sporadic death of large trees caused multiple tree falls with spatially clumped mortality. As a consequence, the findings regarding mortality do not support the postulate of reduced tree stability on slopes. The substantial allocation of wood producing down-slope elliptic trunk cross-sections

(H_3) may in fact efficiently stabilize leaning trees with eccentric crowns.

Furthermore, two studies currently in progress evaluate the effect of slope on the occurrence of dead trees on the forest floor (H_4) as well as the effect of slope on gap frequency (H_5) and showed the following preliminary results:

H_4: The number of dead trees on the forest floor is higher on steep slopes than on flat ground.

H_5: Forests on steep slopes had higher percentage of their area in gap-phase than forests on flat ground and frequency of large gaps (> 125 m^2) was higher.

These preliminary results are in contrast to the findings of equal mortality (H_8), and provide evidence that slopes may have a negative effect on tree stability and enhance probabilities of tree-fall.

In summary, all but the mortality hypothesis (H_8) were supported, causing a marked shift to the right of the logical tree (Fig. 5-1). Given the powerful conclusion of both gap (H_5) and growth (H_6) hypotheses, and despite the failure to support the mortality hypothesis (H_8), I conclude that the oak-bamboo forest of the Upper Rio Macho watershed is more dynamic on slopes than on flat terrain.

Drawing this overall conclusion by means of strong inference is an inductive process (Platt 1964, Poper 1965) that provides at best a sound postulate based on supportive data that needs to be exposed to further testing. For

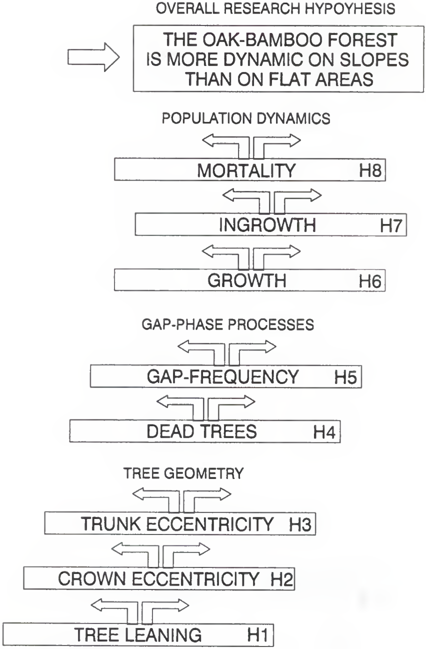


Fig. 5-1. "Logical tree" (Platt 1964) after hypothesis testing. Sufficient evidence emerged to reject the null hypotheses in favor of H_1, H_2, H_3, H_4, H_5, H_6, H_7, producing a shift to the right of the logical tree. The null hypothesis of H_8 could not be rejected, causing a shift to the left. It is inductively concluded that the overall hypothesis is likely to be true.

example, more attention should perhaps be given to the representativeness of the conclusion drawn from the flat portion of the study area. In the rugged landscape of the Upper Rio Macho watershed, flat terrain is not abundant and was only encountered in one area. As a consequence, control plots, to which forest dynamics on slopes was compared, were clustered in space and the reduced dynamics observed on the flat area may be the result of some site specific bias, perhaps not related to topography. Therefore, some key studies, such as growth rates in response to topography, should be conducted in other areas of the Cordillera de Talamanca. However, the fact that intermediate slopes showed "intermediate" results for all tests other than mortality makes this potential segregation effect of the control area on flatter ground less worrisome. Furthermore, the results of the long-term study of mortality will also constitute a crucial test of this postulate.

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BIOGRAPHICAL SKETCH

Pierre O. B. Berner was born on December 12, 1946, in Switzerland. Between alpine skiing, mountain climbing, spelunking and exploring the mixed broadleaf forests of the Piedmont of the Jura, he obtained his high school diploma in 1966, discovering his affinities to biology, geography, geology and mathematics. In 1967 he entered the Department of Forest Engineering of the Federal Polytechnicum in Zurich, where he received his Masters in Forest Science in 1973. He developed interest in ecology and silviculture of tropical forests and attended, at the Federal Polytechnicum in Zurich, a one-year Interdisciplinary Post-Graduate Study in Problems of the Third World with the objective to complement his technical background with social sciences. Between 1974 and 1984 he was long-term Project Leader of several International Development Forestry Projects and intermittent short-term consultant for the Swiss Service for Technical Cooperation in various Latin American countries. He entered the University of Florida in 1984, and conducted fieldwork in Costa Rica between 1987 to 1990 were he was also Coordinator of an International Silviculture Project in natural forest management at the Centro Agricultural Tropical de Investigacion y Ensenanza (CATIE). After graduation he intends to teach and pursue research on tree geometry, forest dynamics and silviculture and hopes to contribute to the field of sustainable forest management.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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